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FINAL REPORT:

RETROSPECTIVE STUDIES OF THE EFFECTS OF GREEN TREE RETENTION ON CONIFER PRODUCTION AND BIODIVERSITY ON THE WILLAMETTE NATIONAL FOREST

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INTRODUCTION

Integration of ecosystem science into policy and practice is one of the fundamental changes occurring in management of federal forests. That living and dead biotic structures can play critical roles in persistence of ecosystems through catastrophic disturbances is one result from ecosystem science that has stimulated changes in management. Among such "legacies" are snags, logs, patterns in soil chemistry, plant propagules, and live trees. Altering timber harvest regimes to leave large, live trees on cutting units has been advocated as an application of the legacy concept. "Green tree retention," as this practice is called, has recently been adopted as policy for federal forest land within the range of the Northern Spotted Owl.

Although green tree retention and other ideas from ecosystem science are being incorporated into forest management, the implications of these changes are uncertain. It is not unusual for new concepts in land management to be implemented as working hypotheses, rather than as confirmed scientific fact. Indeed it is essential that the implementation of new concepts includes continual monitoring, and feedback processes to ensure modifications of management when necessary. At the same time, it is critical to use a variety of methods to estimate promptly the likely effects of green tree retention, rather than waiting for decades of development of managed ecosystems.

We evaluated effects of green tree retention on conifer production and selected aspects of forest biological diversity, using both a retrospective examination of natural stands and studies including operational green tree retention harvest units. The retrospective study was conducted in natural stands that approximated green tree retention cuts projected into the future, in having

residual old-growth trees over regeneration that was near currently accepted rotation age for federal forests (70 - 130 years). Such a retrospective approach provides timely insights into likely consequences of green tree retention. We also worked in recent green tree retention units because some potentially important biological responses to green tree retention are likely to be transitory and may, with time, be overwhelmed by other influences.

Components of biological diversity examined in the retrospective study included vascular plants, forest floor mosses, and epiphytic lichens. Studies in operational green tree retention units examined abundance and distribution of mycorrhizal mats, diversity of ectomycorrhizae on tree seedlings, and diversity and distribution of arthropods. Two alternative analyses were made of the retrospective data on conifer production (see sections by Acker and by Zenner). Data from the retrospective study are stored in the Forest Science Data Bank, Department of Forest Science, Oregon State University, and are accessible contingent on permission of the investigators.

Structure, composition, and dynamics of two-aged forest stands on the Willamette National Forest: a retrospective study concerning green-tree retention

Final report of research carried out under:

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Retrospective Studies on the Effects of Green Tree Retention on Conifer Production and Biodiversity on the Willamette National Forest

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ABSTRACT

Practices developed from ecosystem science, such as green tree retention, are becoming integrated into forest management as working hypotheses, rather than as rigorously established facts. Although in the long run manipulative experiments may provide the most definitive information on the consequences of new practices, in the short term other sources of information are needed. This retrospective study of natural, two-aged forest stands on the Willamette National Forest is intended to provide such information.

Eighteen stands throughout the Forest were sampled, 14 in the western hemlock zone and four in the Pacific silver fir zone. In each stand, adjacent, paired plots were measured, one with residual trees over a younger cohort and one with only the younger cohort. Younger cohort stand ages ranged from 66 to 131 years for plots in the western hemlock zone, and from 82 to 236 years for plots in the Pacific silver fir zone. Characteristics of both the residual trees and the younger cohort were recorded, to describe these stands as natural models for green tree retention, and to estimate quantitative effects of the residual trees on the younger cohort and on the total stand.

The natural, two-aged stands in this study in the western hemlock zone provide a precedent for management with green tree retention. For the majority of the plots with residual trees, live residual tree density was within the range of prescriptions

of recent National Forest plans for western Oregon (*i.e.* 5 to 25 trees per ha, or 2 to 10/ac). Broken and/or dead tops were common among the live residual trees. Although Douglas-fir was the dominant species in the younger cohort, western hemlock was present in most of the plots in the western hemlock zone, whether or not residual trees were present.

For the western hemlock zone stands, basal area, volume, mean annual increment, current volume growth rate of the younger cohort, and basal area growth of the younger cohort plus residual trees all declined with increasing residual tree basal area. These relationships were best described by curvilinear models; the greatest effect per unit residual basal area occurred at low residual tree levels. The relationship between younger cohort mean annual increment (MAI) and estimated basal area of residual trees at the time of establishment of the younger cohort was the strongest pairwise relationship between measures of the younger cohort and the residual stands. For 10 m^2/ha residual tree basal area (44 ft^2/ac; equivalent to about 12 average-sized residual trees per ha for these stands or 5/ac), the regression model for this relationship predicted a decline in younger cohort MAI of 26% (95% confidence interval -30 to -22%). Total live standing volume (younger cohort plus residual) was not significantly correlated with any measure of the residual component of the stands.

The stands in this study were unlike typical Douglas-fir

plantations in important respects. Density of trees was much higher than under a management regime including thinning. The period of time over which the younger cohort became established was much longer than the period allowed under law for contemporary post-harvest stands. These differences complicate application of these results to managed stands, and may indicate ecologically important distinctions between natural and managed stands. Because of the nonlinear relationship between residual tree basal area and younger cohort volume and basal area, extrapolation to larger spatial scales such as cutting units is not straightforward. Extrapolation to larger spatial scales will require a better understanding of the effects of low levels of residual trees on growth of the younger cohort.

INTRODUCTION

Integration of ecosystem science into policy and practice is one of the fundamental changes occurring in management of federal forests (Kessler *et al.* 1992). That living and dead biotic structures can play critical roles in persistence of ecosystems through catastrophic disturbances is one result from ecosystem science that has stimulated changes in management (Franklin 1988, 1989, Swanson and Franklin 1992). Among such "legacies" are snags, logs, patterns in soil chemistry, plant propagules, and live trees (Swanson and Franklin 1992). Altering timber harvest regimes to leave large, live trees on cutting units has been advocated as an application of the legacy concept (*e.g.* Franklin 1989). "Green tree retention," as this practice is called, has recently been adopted as policy for federal forest land within the range of the northern spotted owl (USDA Forest Service and USDI Bureau of Land Management 1994).

Although green tree retention and other ideas from ecosystem science are being incorporated into forest management, the implications of these changes are uncertain (Swanson and Franklin 1992). It is not unusual for new concepts in land management to be implemented as working hypotheses, rather than as confirmed scientific fact (Kessler *et al.* 1992, Franklin 1995). Indeed it is essential that the implementation of new concepts includes continual monitoring, and feedback processes to ensure

modifications of management when necessary (Kessler *et al.* 1992, Franklin 1995). At the same time, it is critical to marshal as much information as possible now, rather than waiting for decades of ecosystem development under new management practices (Thomas *et al.* 1993). To this end, we conducted a retrospective study of natural stands that developed after natural disturbances, as analogues for green tree retention harvest.

In comparing retrospective studies to manipulative, experimental studies, there is a trade-off of timeliness for definitiveness. Interpretation of retrospective data requires assumptions concerning events that resulted in contemporary conditions. These assumptions may be difficult or impossible to test. However, in the case of forest management, retrospective studies can produce information decades before the conclusion of manipulative experiments. Thus, retrospective studies can serve as an efficient means to gain some understanding in the short-term. As such, retrospective studies are a useful complement to experimental studies.

Drawing inferences for managed stands from any study of natural stands requires caution. Conditions during stand development may be quite different, due to management activities such as artificial regeneration of conifers, removal of competing vegetation, and control of tree density. On the other hand, understanding natural ecosystems is a prerequisite to sustainable management of ecosystems (Lubchenco *et al.* 1991, Swanson and

Franklin 1992). Furthermore, natural processes may dominate managed forests in the future as land managers seek to minimize inputs (Swanson and Franklin 1992).

This paper contains my analyses of composition, structure, and dynamics of the tree stratum of natural, two-aged stands on the Willamette National Forest. In addition to providing basic, descriptive data for natural stands that may serve as models for stands managed with green tree retention, my objective is to test several propositions concerning the effect of residual trees on the development of these stands. I tested the effect of the residual trees on standing basal area, basal area of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), tree density, standing volume, volume growth rate, mean annual increment, average height, and an index of tree mortality within the younger cohort of trees beneath the older component of the stands. I also tested the effect of the older component on basal area growth and standing live volume of the younger cohort and older component combined. Other papers in this report contain analyses of other aspects of the vegetation of the natural, two-aged stands (*i.e.* Traut's paper on understory vegetation; Peck and McCune's paper on epiphytic lichens), or analyze the tree stratum with alternate techniques (*i.e.* Zenner's paper).

This study should be considered within the context of an evolving operational definition of green tree retention. In the

late 1980s and early 1990s, green tree retention was commonly described in terms of retained trees per acre (*e.g.* Franklin 1989, Birch and Johnson 1992), often with trees dispersed throughout cutting units (*e.g.* Franklin and Spies 1991). Currently, however, prescriptions for federal timberlands in western Oregon and Washington contain at least two distinct methods of green tree retention (USDA Forest Service and USDI Bureau of Land Management 1994). On Bureau of Land Management lands in Oregon, green tree retention is described by numbers of tree per acre. For most National Forests in western Oregon and Washington, retention is to be achieved primarily by leaving patches of trees, 0.2 hectare (0.5 acre) or larger (USDA Forest Service and USDI Bureau of Land Management 1994). This study concerns natural, two-aged stands with scattered residual trees. Thus this study has no direct applicability to aggregated green tree retention.

METHODS

Site selection

We sought areas within the Willamette National Forest covered by unmanaged forests of 60 to 100 years old (referred to below as "younger cohort"), with scattered large trees that survived the stand-initiating disturbance ("residual trees"). Our sampling design (see below) required that study areas be at least 1 hectare (2.47 acre), and be relatively homogeneous (i.e.

no major slope breaks, drainages, obvious soil differences, or patches of tree mortality). We intended to stratify our sampling on the basis of similar plant associations, as defined by Hemstrom *et al.* (1987). We identified five groups of similar plant associations on which to focus, in order of priority:

1) TSHE/GASH, TSHE/BENE, TSHE/BENE-GASH;

2) TSHE/RHMA-BENE, TSHE/RHMA-GASH, TSHE/RHMA-LIBO;

3) ABGR-ABAM/SMST, ABAM/TITR, ABAM/ACCI/TITR, ABAM/OXOR;

4) PSME/HODI-BENE, PSME/HODI/GRASS, PSME/HODI-WHMO, PSME-TSHE/GASH;

5) TSME/VAME/XETE, TSME/VASC, TSME/LUZULA.

For the first two groups, we intended to measure at least 10 sites per group. We intended to measure sites representing the other groups as time and availability of appropriate locations allowed.

We compiled an extensive list of potential study areas throughout all seven Ranger Districts of the Willamette National Forest drawing on other workers' field observations and analysis of U.S. Forest Service stand examination data (see Acknowledgments). Initial screening was based on written descriptions, air photos, and topographic maps. Final selection of study areas was based on inspection on the ground. Sites were included in the study when it was possible to locate two, 61.8 m diameter circular plots entirely on one topographic feature. In addition, it was required that one of the plots contain large

residual trees and that the other plot lack residual trees.

Sampling design

We used nested, concentric, fixed-radius plots to measure residual trees and the younger cohort. Residual trees were measured in the larger of the plots ("residual plots"), and the younger cohort in the smaller of the plots ("detection plots") (Fig. 1). Nested plots were used to characterize, as completely as possible, the large residual trees that affected the development of the younger cohort. Although it is conceivable that trees may affect one another over very large distances, for the purposes of this study we assumed that the effects of a residual tree on trees in the younger cohort were minimal at and beyond 60 ft (18.29 m), (Hoyer unpub.). We used detection plots of 500 m^2 (5380 ft^2)(radius 12.62m), and residual plots of 3000 m^2 (32,280 ft^2)(radius 30.90m). Plot areas were slope-corrected in the field. Paired residual plots (one with residual trees, one without), were placed as close together as possible,

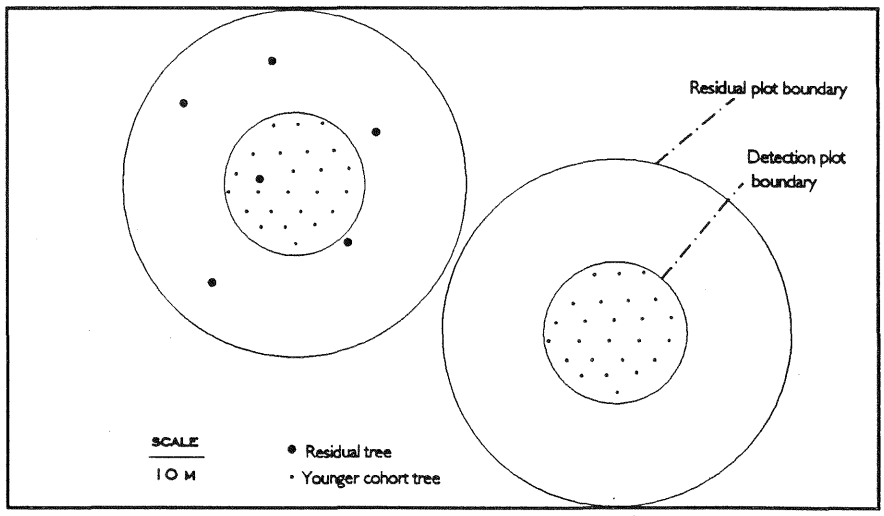

Figure 1. Sample plot layout.

in keeping with the site selection criteria.

Data collection

For each residual plot, various environmental data were recorded in the field or obtained from maps. Slope, aspect, and topographic position (bottom, middle, or top one-third of slope) were recorded in the field. Plant association (Hemstrom *et al.* 1987) was determined from understory plant data (Traut 1994). Elevation was determined from topographic maps. Mapping unit in the Willamette National Forest Soil Resource Inventory (SRI, Legard and Meyer, 1973) was determined from the SRI Atlas.

We recorded species, diameter at breast height (dbh), and location relative to plot center for all trees ≥ 5cm (2 in) dbh, living or dead, residual or younger cohort. Additional measurements varied depending on whether the tree was live or dead, and on whether the tree was a residual or belonged to the younger cohort. All residual trees within the residual plot were measured; younger cohort trees were measured within the detection plot only.

For all live trees, we recorded the condition of the bole and crown using the codes in Table 1. For younger cohort trees, we classified the canopy class relative to all trees in the younger cohort using the categories in Table 2. For residuals we obtained four perpendicular crown radii. We measured total height, and height to base of live crown, for all residuals and a

representative sample of the younger cohort. We extracted increment cores from all residuals and from a representative sample of the younger cohort. We intended to obtain cores of at least 100 years for the residuals and to the pith for younger cohort trees. All cores were taken at breast height.

Dead trees that were measured included residuals of decay classes 1, 2, and 3 (Maser *et al.* 1988), and all dead younger cohort trees. For all these trees, we recorded decay class and bole position (i.e. standing with crown, main stem broken, crushed but still rooted, or uprooted). Total heights were recorded for all dead residual trees.

Segments of downed logs within detection plots were measured. Species, decay class (following Maser *et al.* 1988), end diameters and lengths were recorded. Logs smaller than 10cm in diameter were excluded.

Data have been entered into the electronic Forest Science Data Bank (FSDB), maintained by the Department of Forest Science, Oregon State University. The data are identified in FSDB by the study code "TV033."

Table 1. Bole and crown conditions recorded for live trees. As many as three were recorded for each tree.

Bole conditions	Crown conditions
GOOD STRAIGHT BOLE	CROWN IN GOOD CONDITION
PISTOL BUTT (The base of the tree is curved but the tree has righted itself in a short distance.)	BROKEN TOP
BUTT SWELL--IF ABNORMAL FOR SPECIES	MULTIPLE TOPS OR LEADERS
FORKED OR MULTIPLE BUTT	DEAD TOP
LEANING	UNKNOWN TOP (top not seen)
GROUSE LADDER (An abnormally large number of lower branches remain on the tree.)	HALF-CROWNED (branches on only one side of the stem)
SWEEPING	CROOK IN CROWN
CROOKS IN BOLE	MISTLETOE
CONKS PRESENT	FLAT TOP

Table 2. Canopy class categories recorded for younger cohort trees.

Dominant	Crown emerges from the general canopy layer, and so receives light from the top and the sides
Codominant	Crown extends to the top of the general canopy layer, and so receives light from the top, but not much from the sides
Intermediate	Crown extends into the lower portion of the general canopy layer, and so receives mostly filtered light from the top and the sides
Suppressed	Crown completely beneath the general canopy layer

Data summary

To characterize the plots, describe the residual and younger cohort stand components, and perform statistical tests, various summary statistics were computed. The methods for several of these require some explanation. These include stand age, site index, volume, volume growth rate, and mortality index for the younger cohort, and several measures of the residual stand.

Stand age was defined as the age at breast height of the oldest tree in the younger cohort. Some cores included in the sample of tree ages did not include the pith, but were judged by the curvature of the innermost rings to be within 10 years of the pith. The estimated number of missing rings was added to each of

these ages.

To represent the potential productivity of each study area, I computed King's (1966) Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) site index for plots in the western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) zone, and the high-elevation Douglas-fir site index of Curtis *et al.* (1974) for plots in the Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) zone. For each pair of plots, site trees were selected from the combined sample of younger cohort trees on the plot with residual trees and the plot without residual trees. For King's site index, I used all live Douglas-firs that had measured ages and heights and were larger than the minimum dbh for site trees (a function of stand-level mean dbh, King 1966). For the high elevation site index, I used all live Douglas-firs that had measured ages and heights and were classified as dominants (Curtis *et al.* 1974). Given the potential for residual trees to inhibit height growth of trees in the younger cohort, the site index values may somewhat underestimate site productivity.

Volume of younger cohort trees was computed by different methods for conifers and hardwoods. Conifer volumes were computed following the tarif system (Brackett 1973). The tarif system is a means to select a local volume-basal area relationship for a particular stand and species, based on a subsample of trees with measured diameters and heights (Chambers

and Foltz 1980). For each unique combination of conifer species and plot, I selected all trees with measured heights. Volume was computed for these trees using the coefficients in Table 3 and one of the following two equations:

$$\text{volume} = b_0 * (\text{dbh}^{**}b_1) * (\text{height}^{**}b_2) \quad (1)$$

$$\text{volume} = b_1 * \text{dbh}^2 * \text{height}. \quad (2)$$

From volume and dbh I computed the tarif number for each tree, then calculated the average tarif number for the species and plot. Average tarif numbers were computed separately for each plot (*i.e.* separately for each plot location and for plots with and without residual trees). For all live trees for the species and plot (including those with measured heights), volume was then computed from dbh and average tarif number (Brackett 1973).

Table 3. Volume coefficients used to determine conifer species' plot-level average tarif numbers. All coefficients from Browne (1962) unless otherwise noted.

Species	Equation	b_0	b_1	b_2
Douglas-fir	(1)	0.0000472493	1.739925	1.133187
western hemlock	(1)	0.0000382811	1.842680	1.123661
western red cedar	(1)	0.0000717877	1.720761	1.049976
Pacific silver fir	(1)	0.0000512671	1.806775	1.094665
western yew[1]	(1)	0.0000382811	1.842680	1.123661
incense cedar[2]	(2)		0.2149	
mountain hemlock[2]	(2)		0.2921	
Noble fir[2]	(2)		0.2734	

1--No coefficients available; value for western hemlock used.

2--Coefficient from Forest Science Data Bank, study code TV009 (dendrometer data), Oregon State University. R^2 values and sample sizes are 0.975 and 25 for incense cedar, 0.990 and 399 for mountain hemlock, and 0.993 and 312 for Noble fir.

Hardwood volumes were computed using the equations listed in Table 4. For some individuals of big-leaf maple (*Acer macrophyllum* Pursh) and golden chinkapin (*Castanopsis chrysophylla* (Dougl.) DC), heights were not measured. In these cases, height was estimated from diameter using the appropriate equation from Garman *et al.* (1995).

Table 4. Volume equations for hardwood species. All equations, R^2 values, and sample sizes are from Means *et al.* 1994; dbh and height in meters.

Species	volume equals	R^2	Sample size
big-leaf maple	0.0000246916*(dbh)^(2.35347)*(height)^0.69586	0.924	61
golden chinkapin	0.0000568840*(dbh)^(2.07202)*(height)^0.77467	0.958	60
Pacific dogwood[1]	(exp[4.9883106+2.49990*log(dbh*100)])/(100^3)		
Pacific madrone	0.0000378129*(dbh)^(1.99295)*(height)^1.01532	0.959	58

1--No equation available, equation for red alder (*Alnus rubra* Bong.) used.

Current volume growth rate of Douglas-fir and western hemlock was estimated for all plots in the western hemlock zone. A modified version of the tarif growth multiplier method (Chambers and Foltz 1980) was used. Average tarif number for each species and plot combination was computed as described previously. For each live tree, the growth multiplier (*i.e.* amount of volume growth for a fixed, small increment of diameter) was computed from average tarif number and dbh (Brackett 1973). For each live tree, current average annual diameter growth was defined as one-fifth of the most recent 5-year diameter increment. Current growth was computed as growth multiplier times current average annual diameter growth. Current growth was

summed over all trees in a plot, and converted to m^3/ha/yr.

Increment cores and hence diameter increment data were lacking for 29% of the younger cohort Douglas-firs and western hemlocks (mostly small trees). Using the trees with increment data, missing values were estimated from regressions of 5-year increment on dbh (see Results).

To express tree mortality as a fraction of the younger cohort, I computed a younger cohort mortality index for each plot. Only dead trees of decay classes 1 and 2 were included, since, given their diameters, tallying such trees would approximate the number of trees dying the previous 10 years (Maser et al. 1988). The index was computed as follows:

MI = ((Dead) / (Dead + Live)) * 100

where MI = mortality index;

dead = number of dead younger cohort trees per ha of decay classes 1 and 2; and

live = number of live younger cohort trees per ha.

In quantifying the residual component of the stands, I estimated the quantity of live residual trees at the time of initiation of the younger cohort. Thus, in addition to live trees per ha and basal area per ha, I defined "initial trees per ha" and "initial basal area per ha." Initial trees per ha was calculated as live residual trees, plus snags of decay classes 1, 2, and 3. Our observations of snags more advanced in decay suggested that they died during or prior to the event that

initiated the younger cohort. Estimation of initial residual basal area was based on increment core data from residual trees. However, not all residual trees had cores of sufficient duration. For residual trees with complete increment data, dbh at younger cohort initiation was computed by subtracting twice the appropriate amount of radial increment from current dbh. About 35% of the trees had partial (≤ 50 year) or missing cores (the latter including snags of decay classes 1, 2, and 3). From the trees with complete cores, statistical models were developed to estimate the missing data (see Results). To determine the amount of increment to subtract for snags, time since death was estimated as M_d:

M_d = midpoint of range of age at which each decay class is reached for trees > 48 cm (19 in) (from Maser *et al.* 1988).

M_d = 3, 13, and 35 years for decay classes 1, 2, and 3, respectively. Initial residual basal area was also used to estimate growth of the combined stand on each plot (*i.e.* younger cohort plus residual) since initiation of the younger cohort.

For four of the plots, younger cohort stand age exceeded slightly the total length of residual tree increment data (120 years). A statistical model was also developed to extrapolate back to the initiation of the younger cohort for these plots (see Results).

That many of the residual trees had broken tops was an important consideration in estimation of live volume of the residual stands. Since the taper equation form developed by Kozak (Avery and Burkhart 1983) provides for correction for volume in the missing top, it was used to estimate volume of live residual trees:

$$\text{volume} = (7.85*10^{-5})*(\text{dbh})^2*(b_0*H_1)+(b_1/2)*(H_1^2/H)+(b_2/3)*(H_1^3/H^2)$$

where H = intact height of tree, and

H_1 = current height of tree.

Species-specific coefficients developed from the Forest Science Data Bank dendrometer data (Garman, unpubl.) were used (Table 5). For trees with broken tops, it was necessary to estimate the intact height. These heights were estimated from dbh using the appropriate equations from Garman *et al.* (1995).

Table 5. Coefficients for taper equations used to estimate volume of residual trees. All information from Garman (unpubl.).

Species	b_0	b_1	b_2	R^2	Sample size
Douglas-fir	0.87201	-1.48078	0.60877	0.95	216
western hemlock	1.11125	-1.69534	0.58409	0.85	352
western red cedar	1.19210	-2.38420	1.19210	0.92	53
mountain hemlock	0.94295	-1.46136	0.51841	0.98	420

Crown area of residuals was computed from the average of the four crown radii, assuming circular crowns. Portions of crowns

computed to fall outside of the residual plot boundary were excluded from the calculation.

Data analysis

The primary objective of data analysis was to evaluate the ability of various measures of the residual stand to predict wood production and related attributes of the younger cohort, or the younger cohort and residuals combined. I arranged these variables into two matrices, one of predictor variables and one of response variables. I examined pair-wise correlations within the two matrices, to see which predictors might differ from one another in their power, and which responses might be explained by different predictors. Rather than investigating all possible pairings of predictors and responses, the scheme described below was set up prior to analysis. Due to the small sample size and complex history of plots in the Pacific silver fir zone (see Results), these analyses were restricted to plots in the western hemlock zone.

Response variables were defined to exploit explicitly the paired-plot design. Most of the responses were defined as the percent difference of the value with residual trees relative to the value without residual trees. Using younger cohort volume as an example:

$PD_V_i = ((V_{iW} - V_{iO})/V_{iO}) * 100$

where PD_V_i = the percent difference in younger cohort volume for plot pair i;

V_{iW} = younger cohort volume in plot i with residual trees;

V_{iO} = younger cohort volume in plot i without residual trees.

This was not possible for percent basal area of western hemlock, because western hemlock was not present on some of the plots without residual trees. Thus, I used the absolute differences between the paired plots:

$DF_TS_i = (tsb_{iW}/b_{iW}) - (tsb_{iO}/b_{iO})$

where DF_TS_i = difference in percent hemlock basal area for plot pair i;

tsb_{iW} = younger cohort western hemlock basal area in plot i with residual trees;

b_{iW} = total younger cohort basal area in plot i with residual trees;

tsb_{iO} = younger cohort western hemlock basal area in plot i without residual trees;

b_{iO} = total younger cohort basal area in plot i without residual trees;

The response and predictor variables used in statistical tests are defined in Table 6.

Table 6. Predictor and response variables used in statistical tests of effects of residual trees.

Variable type	Symbol	Definition
Predictor	BA_I	Estimated live basal area of residual trees at time of initiation of younger cohort
Predictor	BA_L	Basal area of live residual trees
Predictor	CRAR	Crown area of residual trees
Predictor	TPHI	Estimated live residual trees per ha at time of initiation of younger cohort
Predictor	TPHL	Live residual trees per ha
Predictor	VOLL	Volume of live residual trees
Response	DF_TS	Absolute difference between paired plots in percent of younger cohort basal area in western hemlock
Response	PD_B	Percent difference between paired plots in younger cohort basal area
Response	PD_BT	Percent difference in younger cohort plus residual basal area growth since initiation of younger cohort
Response	PD_H	Percent difference in average height of younger cohort dominant and codominant tree heights
Response	PD_MA	Percent difference in younger cohort mean annual increment (i.e. (live volume)/(younger cohort age))
Response	PD_MI	Percent difference in younger cohort mortality index
Response	PD_T	Percent difference in younger cohort trees per ha
Response	PD_V	Percent difference in younger cohort volume
Response	PD_VG	Percent difference in younger cohort current volume growth rate, Douglas-fir and western hemlock only
Response	PD_VT	Percent difference in younger cohort plus residual live volume

In outline, the plan of the analysis was to identify the one

predictor variable which was most highly correlated with each response variable. Then each response-predictor pair was evaluated for the applicability of linear regression. Finally, the relationship between younger cohort mean annual increment (MAI) and its most-highly-correlated predictor was evaluated using a smaller radius of influence of residual trees. Thus, the predictor's value was re-computed, including only residual trees within 24.81 m and 18.72 m of the center of the plot. The radius of the detection plot was the same for all analyses (12.62 m). Thus, plot radii of 24.81 m and 18.72 m represent, respectively, inclusion of residual trees up to distances from the edge of the the detection plot two-thirds and one-third of the 18.29 m radius of influence derived from Hoyer (unpub.)(*i.e.* 12.62 m+12.19 m, 12.62 m + 6.10 m).

The relationships between the response and predictor variables were evaluated using linear regression (SAS Institute Inc. 1989). For models that were statistically significant ($P<0.05$), the validity of the underlying assumptions of linearity, equal error variance, and normality of residuals was evaluated by observation of plots of standardized residuals and from the W-test of normality (SAS , Sabin and Stafford 1990). Extreme observations ("outliers") and influential observations (*i.e.* observations with a large influence on parameter values) were identified by computation of studentized residuals and influence statistics (DFFITS and DFBETAS), respectively (SAS

Institute Inc. 1989). Residuals or influence statistics ≥ 2 indicated extreme or influential observations.

Inasmuch as non-linear responses of younger cohort basal area and volume to residual tree density have been suggested (*e.g.* Birch and Johnson 1992, Rose 1993), various curvilinear models were evaluated in addition to the linear model. The curvilinear models fit to the data were:

$$Y = a + b * (1/X)$$

$$1/Y = a + b * X$$

$$Y = a + b * X + c * X^2.$$

These models were selected to permit either a decreasing effect per residual tree (*e.g.* Birch and Johnson 1992) or an increasing effect per residual tree (*e.g.* Rose 1993), and to accommodate negative or zero Y-values and the potential for zero X-values. These models were fit for basal area and volume response variables (*i.e.* all response variables except DF_TS, PD_H, PD_MI, and PD_T) for which the linear model was significant. The linear model and the various curvilinear models were compared on the basis of R^2 and the goodness-of-fit criteria, especially residual plots and occurrence of influential observations and/or outliers.

For all regressions, both slope and intercept were estimated. That is, it was not implicitly assumed that relationships between response and predictor variables would pass through the origin (*i.e.* response=0 when predictor=0). Although

it follows logically from our study design that there would be no difference between paired plots in the absence of residual trees, several fundamental problems would be caused by constraining regressions to pass through the origin. Regression through the origin violates basic assumptions of least squares regression (Neter *et al.* 1983), and so alters the meaning of R^2 and other diagnostic statistics (Lisa Ganio, personal communication). The confidence interval for predictions from regression through the origin is minimized at a value of zero for the predictor variable (Neter *et al.* 1983), unlike standard regression for which the confidence interval is minimized for the mean value of the predictor (Snedecor and Cochran 1980). Thus, at least in this study, regression through the origin would decrease the precision of predictions in the best-sampled portion of the range of predictor variables. Finally, in this study, regression through the origin would represent extrapolation, which risks misinterpretation (Wonnacott and Wonnacott 1977). In particular, regression through the origin requires the assumption that the relationship between response and predictor variables that holds for the observed data range is also valid near the origin, a problematic assumption (Snedecor and Cochran 1980). Declining to force regressions through the origin avoids these problems, and keeps the focus of the analysis on the range of residual stand values actually observed.

Units of measure

Throughout this paper, results are reported in metric units, with English units in parentheses where practical. To facilitate conversion of results to English units, conversion factors are listed in Table 7.

Table 7. Selected conversion factors from metric to English units.

Metric unit	Equivalent amount in English units
1 cm	0.3937 in
1 m	3.281 ft
1 m^2	10.76 ft^2
1 m^3	35.31 ft^3
1 hectare (ha)	2.471 acre (ac)
1 tree/ha	0.4047 tree/ac
1 m^2/ha	4.357 ft^2/ac
1 m^3/ha	14.29 ft^2/ac

RESULTS

Set of plots in two-aged stands on the Willamette National Forest

We accumulated a sample of 18 pairs of plots in two-aged stands, including all but the two southern-most Ranger Districts of the Willamette National Forest (Table 8). The sample consisted of 14 pairs of plots in the western hemlock zone and four pairs of plots in the Pacific silver fir zone (Table 9).

Table 8. Locations of plot pairs within natural, two-aged stands on the Willamette National Forest

Plot	Ranger District	Lati-tude	Longi-tude	Town-ship	Range	Sect.	1/4	1/16
DE02	DETROIT	44.819	121.892	9S	7E	1	SE	
DE06	DETROIT	44.717	122.104	10S	6E	8	SW	SE
DE05	DETROIT	44.628	122.056	11S	6E	10	SE	NE
DE08	DETROIT	44.626	122.032	11S	6E	11	SE	SE
SH09	SWEETHOME	44.398	122.239	13S	5E	32	NW	SE
SH13	SWEETHOME	44.397	122.247	13S	5E	32	NW	SW
SH12	SWEETHOME	44.393	122.147	13S	5E	36	SE	NE
BR07	BLUE RIVER	44.234	122.289	15S	4E	26	NE	SW
BR08	BLUE RIVER	44.231	122.284	15S	4E	26	NE	SE
MC03	MCKENZIE	44.198	122.208	16S	5E	4	SW	SE
MC04	MCKENZIE	44.194	122.209	16S	5E	9	NW	SE
BR09	BLUE RIVER	44.190	122.280	16S	4E	12	NW	SW
BR17	BLUE RIVER	44.087	122.214	17S	5E	21	NW	NE
LO01	LOWELL	43.978	122.453	18S	3E	28	NE	SW
LO07	LOWELL	43.804	122.613	20S	2E	30	NE	SW
LO06	LOWELL	43.807	122.647	20S	1E	25	NW	NW

Plot	Ranger District	Lati-tude	Longi-tude	Town-ship	Range	Sect.	1/4	1/16
LO05	LOWELL	43.805	122.642	20S	1E	25	NW	SE
LO08	LOWELL	43.801	122.653	20S	1E	26	SE	NE

Plots in the western hemlock zone represented a fairly narrow range of environments, at least as indicated by plant associations (Table 9). All but one of the pairs of plots belonged to the TSHE/BENE or closely related TSHE/BENE-GASH plant associations. Western hemlock plant associations with various mixtures of dwarf Oregon grape (*Berberis nervosa* Pursh) and salal (*Gaultheria shallon* Pursh) in the understory are very common on the Willamette National Forest, and blend into one another along a moisture gradient (Hemstrom *et al.* 1987). The final pair of plots belonged to the TSHE/RHMA-BENE plant association. Although abundance of western rhododendron (*Rhododendron macrophyllum* G. Don) generally indicates unproductive soils, productivity of the TSHE/RHMA-BENE plant association is comparable to the TSHE/BENE to TSHE/GASH gradient (Hemstrom *et al.* 1987). In any case, due to a sample size of one for plots from rhododendron-dominated plant associations, all plots from the western hemlock zone were analyzed as a group.

As indicated by site index of the younger cohort, plots in the western hemlock zone included a wide range of productivity levels (Table 9). Site index ranged from 64 to 114; only three

of the pairs of plots had values as high as the averages for their plant association in Hemstrom *et al.* (1987). Paired plots represented site class 3 (seven pairs), site class 4 (six pairs), and site class 5 (one pair) (King 1966).

Table 9. Environmental and ecological characteristics of plots.

Plot	W/O[1]	Elev (m)	Aspect (°)	Slope (%)	Topo[2]	SRI[3]	Zone[4]	Pl. assoc.[5]	Site index[6]	Resid tph[7]	Stand age	Log vol.[8]
BR07	W	823	14	85	B	210	TSHE	TSHE/BENE	76	33	118	303
BR07	O	823	29	60	B	210	TSHE	TSHE/BENE	76		131	132
BR08	W	823	350	75	B	201	TSHE	TSHE/BENE-- TSHE/RHMA-BENE	64	57	125	66
BR08	Z	823	343	80	B	201	TSHE	TSHE/BENE-- TSHE/RHMA-BENE	64		124	109
BR09	W	671	210	75	T	8	TSHE	TSHE/BENE	97	13	75	243
BR09	O	671	217	68	T	8	TSHE	TSHE/BENE	97		83	294
BR17	W	853	225	73	T	610	TSHE	TSHE/BENE	94	23	90	474
BR17	O	853	230	77	T	610	TSHE	TSHE/BENE	94		64	66
DE06	W	640	143	30	M	212	TSHE	TSHE/BENE	102	17	93	209
DE06	O	640	153	40	M	212	TSHE	TSHE/BENE	102		72	172
LO01	W	731	128	62	T	21	TSHE	TSHE/BENE-GASH	85	37	67	11
LO01	O	731	120	55	T	21	TSHE	TSHE/BENE-GASH	85		66	184
LO05	W	701	102	28	T	212	TSHE	TSHE/BENE	99	53	87	130
LO05	O	701	110	17	T	212	TSHE	TSHE/BENE	99		95	201
LO06	W	701	288	50	T	212	TSHE	TSHE/BENE	114	10	88	217
LO06	O	701	282	35	T	212	TSHE	TSHE/BENE	114		94	493
LO07	W	518	155	10	T	253	TSHE	TSHE/BENE-GASH	90	13	97	605

Table 9, continued.

Plot	W/O[1]	Elev (m)	Aspect (°)	Slope (%)	Topo[2]	SRI[3]	Zone[4]	Pl. assoc.[5]	Site index[6]	Resid tph[7]	Stand age	Log vol.[8]
LO07	O	518	142	17	T	253	TSHE	TSHE/BENE-GASH	90		94	617
LO08	W	792	124	60	T	202	TSHE	TSHE/BENE-GASH	100	10	88	458
LO08	O	792	112	57	T	202	TSHE	TSHE/BENE-GASH	100		90	231
MC03	W	701	220	32	T	23	TSHE	TSHE/BENE-GASH	111	3	90	306
MC03	O	701	230	32	T	23	TSHE	TSHE/BENE-GASH	111		76	162
MC04	W	671	180	33	M	23	TSHE	TSHE/BENE-GASH	108	10	98	103
MC04	O	671	193	25	M	23	TSHE	TSHE/BENE-GASH	108		102	255
SH09	W	671	181	53	T	8	TSHE	TSHE/BENE	89	7	85	187
SH09	O	671	172	70	T	8	TSHE	TSHE/BENE	89		87	97
SH13	W	640	194	30	M	337	TSHE	TSHE/RHMA-BENE	89	13	85	238
SH13	O	640	199	30	M	337	TSHE	TSHE/RHMA-BENE	89		86	203
DE02	W	1219	66	62	T	n/a	ABAM	ABAM/BENE	108	27	82	296
DE02	O	1219	56	60	T	n/a	ABAM	ABAM/BENE	108		83	426
DE05	W	1341	38	40	T	203	ABAM	ABAM/RHMA/XETE	96[9]	73	235	257
DE05	O	1341	45	38	T	203	ABAM	ABAM/RHMA/XETE	96[9]		236	106
DE08	W	1280	65	43	T	167	ABAM	ABAM/TITR	116	27	88	448
DE08	O	1280	73	42	T	167	ABAM	ABAM/TITR	116		88	485
SH12	W	1219	144	30	T	13	ABAM	ABAM/ACCI/TITR	141	17	100	119
SH12	O	1219	150	33	T	13	ABAM	ABAM/ACCI/TITR	141		107	46

Table 9, continued.

1--W = plot with residual trees; O = plot without residual trees.

2--Topographic position: T = top one-third of slope; M = middle one-third of slope; B = bottom one-third of slope.

3--Mapping unit in Willamette National Forest Soil Resource Inventory (Legard and Meyer 1973).

4--Vegetation zone: TSHE = western hemlock zone; ABAM = Pacific silver fir zone.

5--Plant association in the system of Hemstrom *et al.* (1987).

6--King's (1966) 50-year Douglas-fir site index for western hemlock zone; high elevation 100-year Douglas-fir site index of Curtis *et al.* (1974) for Pacific silver fir zone.

7--Live residual trees per ha.

8--Volume of downed logs, m^3/ha.

9--No Douglas-fir site trees on either paired plot; listed site index is average for plant association from Hemstrom *et al.* 1987.

Density of live residual trees covered a broad range, from three to 57 per ha (one to 23 per ac). This is a somewhat broader range than green tree retention prescriptions in recent National Forest plans for western Oregon (Birch and Johnson 1992); for the majority of the plots, live residual tree density falls within the range of the green tree retention prescriptions (i.e., 5 to 25 trees per ha)(Fig. 2.).

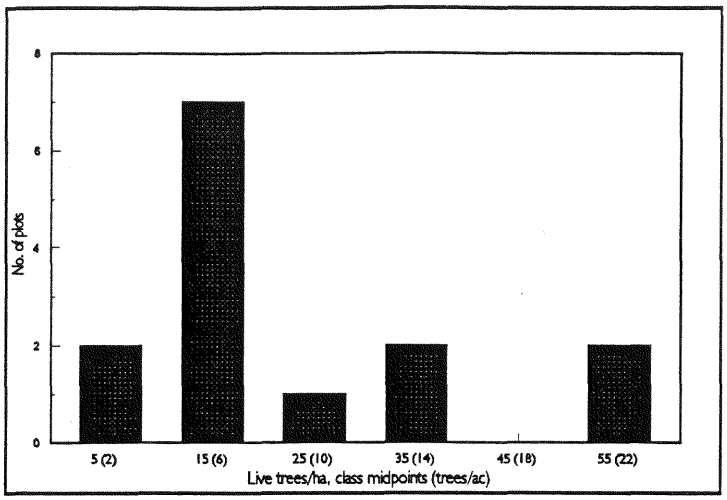

Figure 2. Frequency distribution of live residual trees, western hemlock zone.

Younger cohort stand ages ranged from 66 to 131 years, and were similar within pairs (Table 9). Within pairs, plots had the same elevation and topographic position, and were quite similar in slope and aspect (Table 9). From the Soil Resource Inventory, soils at most of the plots were derived from tuffs and breccias, and range from shallow to deep.

In contrast to the plots in the western hemlock zone, plots in the Pacific silver fir zone represented a diverse set of environments, judging by plant associations (Table 9). The four pairs of plots represented two typically herb-poor and unproductive plant associations (ABAM/RHMA/XETE and ABAM/BENE) and two typically herb-rich and productive plant associations

(ABAM/TITR and ABAM/ACCI/TITR). The productivity differences predicted from the plant associations were borne out in the high-elevation Douglas-fir site index, at least for the three pairs of plots with Douglas-fir site trees (Table 9). Density of live residual trees ranged from 17 to 73 per ha.

Younger cohort stand ages ranged from 82 to 236 years, apparently indicating that it is more difficult to judge stand history from stand structure in the Pacific silver fir zone (Table 9). Stand ages were quite similar within plot pairs. As for the western hemlock zone plots, pairs had the same elevation and topographic position, and were quite similar in slope and aspect (Table 9). Soils at the three of the plots within the area of the Soil Resource Inventory vary in both depth and parent materials.

Descriptive statistics--Residual trees

In the western hemlock zone, the residual component of the stands ranged from a small fraction to more than half of values expected for mature or old-growth stands. Live basal area ranged from about 5 to 48 m^2 per ha (22 to 209 ft^2/ac), compared to average values for mature and old-growth forest of 59 and 69, respectively (257 and 301 ft^2/ac)(Spies and Franklin 1991) (Table 10). Live volume, including top and stump, ranged from about 100 to almost 840 m^3 per ha (1430 to 12000 ft^3/ac). For the predominantly mature and old-growth plots that Hemstrom *et al.*

(1987) used to characterize these plant associations, average volume ranged from about 950 to 1150 m^3 per ha (to 4 inch top)(13600 to 16400 ft^3/ac). Live crown area ranged from about 300 to 5300 m^2 per ha. Thus, if there were no overlap of crowns of residual trees, the projected cover of their crowns would have varied between 3 and 53 percent. Damaged tops were common among the residual trees; over all the plots in the western hemlock zone 39 percent of residual trees had broken and/or dead tops. Average 100-year radial growth ranged from about 5 to 18 cm (2 to 7 in). Average dbh of live residual trees was 105 cm (41.3 in)(range of plot-level averages 71 to 167 cm). Nearly all the residual trees were Douglas-firs (90% of stems and 97% of basal area); the remainder were western hemlock (9% of stems and 2.6% of basal area) and western redcedar.

In the Pacific silver fir zone, the residual component of the stands represented a smaller range of values. Live basal area ranged from about 14 to 31 m^2 per ha (61 to 135 ft^2/ac) (Table 11). For the predominantly mature and old-growth plots Hemstrom *et al.* (1987) used to characterize these plant associations, average basal area ranged from 66 to 84 m^2 per ha (290 to 370 ft^2/ac). Live volume of residuals on our plots ranged from about 190 to almost 350 m^3 per ha (2720 to almost 6420 ft^3/ac). Live crown area for all the plots with residual trees was between 1500 and 1700 m^2 per ha. As in the western hemlock zone, damaged tops were common among the residual trees;

over all the plots 40% of residual trees had broken and/or dead tops. Average dbh of live residual trees was 84 cm (33.1 in)(range of plot-level averages 80 to 115 cm). Most of the residual trees were Douglas-firs (74% of stems and 83% of basal area); the remainder were mountain hemlock.

Table 10. Attributes of the residual stand component, plots in the western hemlock zone.

Plot	Trees per ha		Basal area (m^2/ha)		Live volume (m^3/ha)	Crown area (m^2/ha)	Percent with broken and/or dead tops	Average 100-year radial increment, cm (sample size)
	initial[1]	live	initial[1]	live				
BR07	56.7	33.3	32.3	24.9	376.3	1183	60	7.0 (9)
BR08	63.3	56.7	12.8	23.8	345.2	2305	12	10.8 (14)
BR09	26.7	13.3	29.1	15.7	269.5	1206	75	9.0 (3)
BR17	33.3	23.3	31.9	26.8	475.8	1054	57	5.2 (7)
DE06	16.7	16.7	7.8	13.9	213.8	1659	20	7.5 (2)
LO01	36.7	36.7	15.5	26.0	447.3	3078	36	16.2 (9)
LO05	53.3	53.3	20.9	48.3	836.7	5288	31	18.0 (10)
LO06	10.0	10.0	17.6	23.0	481.6	1595	0	11.9 (2)
LO07	16.7	13.3	22.3	19.5	329.6	1679	25	5.6 (3)
LO08	10.0	10.0	15.7	19.0	356.0	1298	100	7.5 (3)
MC03	3.3	3.3	3.5	4.6	101.7	287	0	8.2 (1)
MC04	10.0	10.0	7.1	9.6	168.6	1030	67	9.2 (3)
SH09	6.7	6.7	4.9	7.0	103.5	670	50	7.7 (1)
SH13	20.0	13.3	22.3	17.7	313.7	1125	100	4.9 (4)

1--Estimated live residual trees/ha and basal area at time of initiation of yonger cohort.

Table 11. Attributes of the residual stand component, plots in the Pacific silver fir zone.

Plot	Trees per ha (live)	Basal area (live) (m^2/ha)	Live volume (m^3/ha)	Crown area (m^2/ha)	Percent with broken and/or dead tops
DE02	26.7	13.7	191.4	1520	37
DE05	73.3	31.1	347.8	1667	36
DE08	26.7	21.1	349.5	1672	75
SH12	16.7	17.5	269.2	1607	0

Descriptive statistics--Younger cohort

In the western hemlock zone plots, most younger cohort trees were Douglas-firs or western hemlocks (Tables 12, 13). Over all the plots, Douglas-fir accounted for 59% of stems and 81% of basal area; western hemlock accounted for 37% of stems and 17% of basal area. Douglas-fir was more ubiquitous than western hemlock: Douglas-fir was in all but one plot whereas hemlock was absent from seven of the 28 plots. Other conifer species present, in decreasing order of abundance, were western red cedar (*Thuja plicata* Donn.), incense cedar (*Calocedrus decurrens* Florin.), and western yew (*Taxus brevifolia* Nutt.). Hardwood species, in decreasing order of abundance, were golden chinkapin, bigleaf maple, Pacific dogwood (*Cornus nuttalli* Aud.), and Pacific madrone (*Arbutus menziesii* Pursh).

For the most part, plots without residual trees had more younger cohort trees and basal area than the paired plots with residual trees (Tables 12 and 13). Number of trees per ha was larger without residual trees in 10 of the 14 pairs. Younger cohort basal area was greater without residual trees in 13 of the 14 pairs.

Table 12. Younger cohort tree density by species, plots in the western hemlock zone (trees per ha).

Plot	W/O	Total	Douglas-fir	W. hemlock	Other con.	Hardwoods
BR07	W	860	0	820	40	0
BR07	O	1380	500	800	80	0
BR08	W	1480	160	1260	60	0
BR08	O	1920	340	1580	0	0
BR09	W	900	860	20	0	20
BR09	O	600	600	0	0	0
BR17	W	900	880	0	0	20
BR17	O	1040	840	0	40	160
DE06	W	680	640	0	20	20
DE06	O	860	840	20	0	0
LO01	W	940	400	540	0	0
LO01	O	1240	920	60	20	240
LO05	W	460	160	240	0	60
LO05	O	847	423	423	0	0
LO06	W	480	160	300	0	20
LO06	O	920	260	660	0	0
LO07	W	660	260	400	0	0
LO07	O	800	360	380	60	0
LO08	W	860	420	440	0	0
LO08	O	680	680	0	0	0
MC03	W	480	420	20	0	40
MC03	O	440	420	0	0	20
MC04	W	620	540	60	0	20
MC04	O	740	640	60	0	40
SH09	W	860	720	60	20	60
SH09	O	1000	1000	0	0	0
SH13	W	1200	500	660	0	40
SH13	O	860	520	260	40	40

Table 13. Younger cohort tree basal area by species, plots in the western hemlock zone (m^2 per ha).

Plot	W/O	Total	Douglas-fir	W. hemlock	Other conifers	Hardwoods
BR07	W	35.6	0.0	35.4	0.2	0.0
BR07	O	79.7	51.9	22.5	5.2	0.0
BR08	W	42.8	9.8	27.6	5.3	0.0
BR08	O	61.0	23.8	37.2	0.0	0.0
BR09	W	51.3	50.7	0.2	0.0	0.4
BR09	O	63.7	63.7	0.0	0.0	0.0
BR17	W	46.7	46.5	0.0	0.0	0.2
BR17	O	63.3	58.5	0.0	0.9	3.9
DE06	W	64.0	63.2	0.0	0.1	0.7
DE06	O	68.6	68.5	0.1	0.0	0.0
LO01	W	39.9	25.6	14.3	0.0	0.0
LO01	O	56.4	51.1	0.3	0.1	4.8
LO05	W	38.1	13.3	21.9	0.0	3.0
LO05	O	65.6	51.1	14.6	0.0	0.0
LO06	W	47.3	22.8	23.3	0.0	1.1
LO06	O	65.6	36.2	29.4	0.0	0.0
LO07	W	47.4	39.7	7.7	0.0	0.0
LO07	O	82.0	54.1	23.8	4.1	0.0
LO08	W	52.0	44.3	7.7	0.0	0.0
LO08	O	74.5	74.5	0.0	0.0	0.0
MC03	W	84.7	84.4	0.1	0.0	0.2
MC03	O	59.7	59.2	0.0	0.0	0.5
MC04	W	58.6	57.7	0.7	0.0	0.2
MC04	O	86.5	86.0	0.3	0.0	0.2
SH09	W	75.7	73.7	0.5	0.2	1.4
SH09	O	83.0	83.0	0.0	0.0	0.0
SH13	W	47.2	32.0	14.3	0.0	1.0
SH13	O	60.2	50.4	8.5	0.5	0.8

Volume of the younger cohort was variable in amount but consistent in domination by conifers (Table 14). Volume ranged from 335 to over 1200 m^3/ha (4790 to over 17000 ft^3/ac). Hardwoods accounted for at most 5% of the volume, in most cases much less. As for basal area, volume was greater without residual trees in 13 of the 14 pairs. Younger cohort mean annual increment ranged from 2.7 to 12.0 m^3/ha/yr (39 to 170 ft^3/ac/yr). MAI was greater without residual trees in 13 of the 14 pairs. Total live volume on plots with residual trees ranged from about 700 to about 1350 m^3/ha (10000 to 19300 ft^3/ac)(Table 14).

Table 14. Younger cohort tree volume, MAI, and younger cohort plus live residual volume, plots in the western hemlock zone (wood volume, including top and stump, m^3/ha).

Plot	W/O	Younger cohort volume			Younger cohort MAI ($m^3/ha/yr$)	Young plus residual volume
		Total	Conifer	Hardwood		
BR07	W	334.8	334.8	0.0	2.7	711.1
BR07	O	725.8	725.8	0.0	5.2	725.8
BR08	W	362.3	362.3	0.0	2.7	707.5
BR08	O	513.5	513.5	0.0	3.9	513.5
BR09	W	495.3	492.3	3.0	6.0	764.8
BR09	O	754.3	754.3	0.0	8.3	754.3
BR17	W	448.0	447.1	0.9	4.6	923.8
BR17	O	649.2	618.3	30.9	9.0	649.2
DE06	W	816.6	811.3	5.3	8.1	1030.4
DE06	O	874.1	874.1	0.0	10.9	874.1
LO01	W	404.7	404.7	0.0	5.4	852.0
LO01	O	614.6	578.6	36.0	8.3	614.6
LO05	W	516.3	483.6	32.7	5.4	1353.0
LO05	O	842.7	842.7	0.0	8.2	842.7
LO06	W	597.6	585.5	12.1	6.2	1079.2
LO06	O	977.9	977.9	0.0	9.6	977.9
LO07	W	586.8	586.8	0.0	5.6	916.4
LO07	O	984.2	984.2	0.0	9.6	984.2
LO08	W	618.3	618.3	0.0	6.4	974.3
LO08	O	944.3	944.3	0.0	9.6	944.3
MC03	W	1173.2	1171.9	1.2	12.0	1274.9
MC03	O	854.4	851.5	3.0	10.2	854.4
MC04	W	887.2	886.1	1.2	8.4	1055.8
MC04	O	1212.2	1210.9	1.3	11.0	1212.2
SH09	W	865.1	855.1	10.0	9.3	968.6
SH09	O	942.7	942.7	0.0	9.9	942.7
SH13	W	441.3	432.2	9.2	4.7	755.0
SH13	O	597.7	592.2	5.5	6.4	597.7

Although mean height of dominant and codominant conifers varied substantially between plots, there was not a consistent difference between paired plots (Table 15). Means varied from about 24 to 43 m (79 to 140 ft). Mean height was greater with residual trees for seven of the 14 pairs of plots.

Of the potential crown and bole anomalies, half-crown was the only one encountered frequently (Table 15). Over all the plots in the western hemlock zone, 19% of the younger cohort trees had half-crowns. The percentage was higher in plots with residual trees in eight of the 14 pairs of plots.

From the sample of younger cohort trees that were cored, the period of recruitment of the current stand varied markedly between plots (Table 15). The range of ages of younger cohort trees varied from nine to 67 years. The age range was larger in plots with residual trees in eight of the 14 pairs of plots.

The number of standing dead trees in the younger cohort also varied substantially between plots, from 80 to 940 trees per ha (32 to 381 trees/ac)(Table 15). The density of dead trees was higher in plots without residual trees in eight of the 14 pairs of plots.

Table 15. Additional characteristics of the younger cohort, plots in the western hemlock zone.

Plot	W/O	Mean height[1]	Percent half-crowned[2]	Age range of live trees, years (sample size)	Number of dead trees per ha
BR07	W	27.2	16	63 (9)	440
BR07	O	29.8	30	67 (22)	500
BR08	W	27.2	28	42 (10)	620
BR08	O	24.3	31	37 (15)	720
BR09	W	29.4	38	24 (10)	300
BR09	O	37.8	37	14 (14)	240
BR17	W	30.4	11	49 (20)	360
BR17	O	29.5	23	14 (19)	500
DE06	W	36.6	26	17 (11)	320
DE06	O	36.1	16	9 (10)	400
LO01	W	31.5	17	19 (11)	780
LO01	O	33.1	10	33 (6)	940
LO05	W	36.6	9	10 (9)	200
LO05	O	38.1	5	22 (17)	360
LO06	W	38.3	8	19 (12)	240
LO06	O	43.3	4	31 (10)	200
LO07	W	37.6	6	12 (6)	340
LO07	O	37.7	0	22 (6)	160
LO08	W	37.7	14	52 (16)	260
LO08	O	38.8	18	23 (17)	320
MC03	W	42.0	42	24 (9)	220
MC03	O	41.4	9	9 (10)	80
MC04	W	41.4	19	30 (12)	240
MC04	O	40.8	32	14 (13)	140
SH09	W	33.8	16	32 (21)	340
SH09	O	32.5	34	36 (20)	280

Plot	W/O	Mean height[1]	Percent half-crowned[2]	Age range of live trees, years (sample size)	Number of dead trees per ha
SH13	W	32.2	10	33 (18)	220
SH13	O	30.2	9	26 (22)	240

1--Mean height of dominant and codominant conifers in meters.

2--Percentage of live trees with half crowns

In the Pacific silver fir zone plots, five conifer species were relatively abundant in the younger cohort (Tables 16, 17). Over all the plots, Pacific silver fir comprised the largest number of stems (36%), followed by western hemlock (22%), mountain hemlock (*Tsuga mertensiana* (Bong.) Carr., 18%), Noble fir (*Abies procera* Rehder, 14%), and Douglas-fir (9%). The order of species was nearly reversed for basal area. Douglas-fir had more basal area than any other species (37% over all the plots), followed by Noble fir (23%), Pacific silver fir (17%), western hemlock (14%), and mountain hemlock (6%). Pacific silver fir was the only species which occurred on all eight plots.

Quantitative comparison between paired plots revealed different patterns depending on the type of data (*i.e.* trees per ha vs. basal area vs. volume). In all four pairs of plots, there were more trees in the plots without residual trees, by as much as a factor of two (Table 16). In the three of the four pairs, the plot without residual trees had more basal area in the younger cohort. However, live volume of the younger cohort was

larger on the plot with residual trees for three of the four pairs of plots (Table 18). For these pairs of plots, the smaller number of trees in the plots with residual trees was apparently more than offset by larger trees (*cf.* Table 16, 17).

Compositional differences were apparent between paired plots, although these varied from pair to pair. At plot DE02, western hemlock was the dominant younger cohort tree with residual trees; Douglas-fir was the dominant younger cohort tree without residual trees. At DE05, Pacific silver fir dominated the plot with residual trees; mountain hemlock dominated the plot without residual trees. The two plots were similar in composition at DE08, with the exception that the plot without residual trees had a Douglas-fir component that was not present on the plot with residual trees. Finally, the two plots at SH12 were very similar with respect to numbers of trees. Based on the species-by-species differences in basal area, individuals of Pacific silver fir and western hemlock were larger in the plot with residual trees, whereas the Douglas-firs were larger in the plot without residual trees.

Table 16. Younger cohort tree density by species, plots in the Pacific silver fir zone (trees per ha).

Plot	W/O	Total	Pacific silver fir	Western hemlock	Mountain hemlock	Noble fir	Douglas-fir	Western red cedar
DE02	W	1860	280	1300	0	220	60	0
DE02	O	2880	500	1660	0	300	380	40
DE05	W	2520	1900	40	580	0	0	0
DE05	O	4680	2240	0	2440	0	0	0
DE08	W	980	340	0	0	640	0	0
DE08	O	1980	560	180	0	1080	160	0
SH12	W	700	80	180	0	0	440	0
SH12	O	780	80	220	0	0	480	0

Table 17. Younger cohort tree basal area by species, plots in the Pacific silver fir zone (m^2 per ha).

Plot	W/O	Total	Pacific silver fir	Western hemlock	Mountain hemlock	Noble fir	Douglas-fir	Western red cedar
DE02	W	69.2	7.3	43.5	0.0	15.7	2.6	0.0
DE02	O	64.9	4.8	19.2	0.0	9.1	31.5	0.3
DE05	W	33.7	31.2	0.1	2.5	0.0	0.0	0.0
DE05	O	46.0	19.4	0.0	26.6	0.0	0.0	0.0
DE08	W	65.3	10.2	0.0	0.0	55.1	0.0	0.0
DE08	O	77.0	8.7	1.4	0.0	55.4	11.5	0.0
SH12	W	69.1	3.2	7.6	0.0	0.0	58.4	0.0
SH12	O	88.2	0.4	2.8	0.0	0.0	84.9	0.0

Table 18. Younger cohort tree volume, MAI, and younger cohort plus live residual volume, plots in the Pacific silver fir zone (wood volume, including top and stump, m^3/ha).

Plot	W/O	Younger cohort		Young plus residual volume
		Volume	MAI (m^3/ha/yr)	
DE02	W	653.9	7.3	845.3
DE02	O	446.1	4.9	446.1
DE05	W	175.5	0.7	523.3
DE05	O	147.9	0.6	147.9
DE08	W	651.6	6.8	1001.1
DE08	O	585.6	6.1	585.6
SH12	W	692.0	6.4	961.2
SH12	O	1122.3	9.8	1122.3

The mean height of dominant and codominant conifers varied substantially between plots, from about 11 to 39 m (36 to 130 ft)(Table 19). Mean height was greater with residual trees for three of the four pairs of plots.

None of the potential crown and bole anomalies were encountered frequently in the Pacific silver fir zone. The most common over all the plots were sweeping boles (6%) and half-crowns (4%).

For three of the four pairs of plots, the range of ages of younger cohort trees was similar to the age ranges for the western hemlock zone plots (*i.e.* 11 to 43 years, Table 19). For plot DE05 however, ages of younger cohort trees spanned nearly

two centuries in both of the paired plots.

The density of standing dead trees in the younger cohort varied from 20 to 1400 trees per ha (8 to 570 trees/ac)(Table 19). For all four pairs of plots the density was higher in the plot without residual trees.

Table 19. Additional characteristics of the younger cohort, plots in the Pacific silver fir zone.

Plot	W/O	Mean height[1]	Age range of live trees, years (sample size)	Number of dead trees per ha
DE02	W	25.4	11 (15)	1180
DE02	O	25.1	25 (14)	1240
DE05	W	17.8	179 (17)	20
DE05	O	10.6	186 (16)	120
DE08	W	29.9	20 (13)	1360
DE08	O	25.7	23 (14)	1400
SH12	W	34.9	43 (16)	260
SH12	O	38.8	32 (15)	500

1--Mean height of dominant and codominant conifers in meters.

Prediction of missing increment data

Two response variables, younger cohort plus residual basal area growth and younger cohort current volume growth rate, required increment core data for every live tree of the younger cohort and living and dead residual trees. Since increments were obtained for most, but not all, of these trees, I developed statistical relationships from the trees with increment data to

predict the missing values. Inasmuch as statistical tests were limited to the set of plots for the western hemlock zone, statistical relationships for missing increment data were likewise restricted to the western hemlock zone.

Current volume growth rate of the younger cohort required the most recent five-year increment. Overall, these increments were measured for 71% of the younger cohort trees (50% of suppressed trees, 80% of intermediate trees, 87% of codominant trees, and 92% of dominant trees). From scatter plots of five-year diameter increment versus dbh, it was clear that there was a strong, positive relationship between the two. Multiple regression models with diameter and categorical variables (canopy class, presence or absence of residual trees, plot location) were evaluated separately for Douglas-fir and western hemlock. For Douglas-fir, the best model included dbh and plot location as predictors ($F=43.7$, $p<0.0001$, $R^2=68\%$, RMSE=2.24, $n=589$). For western hemlock, the best model included dbh only ($F=335.3$, $p<0.0001$, $R^2=58\%$, RMSE=2.05, $n=248$).

To estimate total basal area growth (*i.e.* residual component plus the younger cohort) since initiation of the younger cohort, 100-year increments for all residual trees (*i.e.* live trees and snags of decay classes 1, 2, and 3) were required. Overall, these increments were measured for 65% of the residual trees; incomplete or missing data included live trees with 50-year increments (12%), live trees without increment data (5%), and

snags (all without measured increments, 18% of the residual trees). Separate models were developed for trees with partial increment data and trees with no increment data. For trees with partial increments, the linear regression model of first 50-year increment predicted by most recent 50-year increment was acceptable ($F=188.5$, $p<0.0001$, $R^2=75\%$, RMSE=1.70, $n=63$). The relationship between 100-year increment and dbh, alone and in combination with plot location, was too weak to use for prediction of increment for trees with no increment data. However, mean 100-year increment of Douglas-fir was significantly different between plot locations (analysis of variance: $F=6.7$, $p<0.0001$, MSE=19.6, $n=41$). Thus, Douglas-firs without increment data were assigned the mean 100-year increment for the plot location. The one residual western hemlock without a measured 100-year increment was assigned the mean increment of the other seven residual hemlocks.

For comparison of total basal area growth, younger cohort age was converted from age at breast height to total age by addition of nine years (King 1966). As a result, younger cohort age exceeded the 120 years of residual tree increment data for two of the plots with residual trees (Table 9). For the residual trees with 120 year increment data, the first 20 years' increment was estimated from the subsequent 100 years' increment using linear regression ($F=72.7$, $p<0.0001$, $R^2=54\%$, RMSE=0.96, $n=65$). This relationship was used to predict the radial growth for the

20-year period prior to the measured interval.

Correlations within and between response and predictor variable matrices

Most of the predictor measures were significantly positively correlated with one another, although the strength of the correlation varied from pair to pair (Table 20). The strongest pairwise correlations were between BA_L and VOLL (r=0.98) and between TPHL and TPHI (r=0.94). All of the non-significant pairwise correlations were between BA_I and other predictors. BA_I was significantly correlated only to BA_L.

Table 20. Pairwise Pearson correlation coefficients between predictor variables. Sample size was 14 in all cases.

	BA_I[1]	BA_L	CRAR	TPHI	TPHL
BA_I[2]					
BA_L	0.54*				
CRAR	0.14	0.87***			
TPHI	0.50	0.72**	0.59*		
TPHL	0.26	0.77**	0.77**	0.94***	
VOLL	0.52	0.98***	0.84***	0.59*	0.66**

1--*** = p<0.001; ** = p<0.01; * = p<0.05

2--BA_I=estimated basal area of live residual trees at initiation of younger cohort; BA_L=basal area of live residual trees; CRAR=crown area of residual trees; TPHI=estimated live residual trees per ha at initiation of younger cohort; TPHL=live residual trees per ha; VOLL=volume of live residual trees.

Most of the pair-wise correlations between response measures were not significant (Table 21). However, correlations between the younger cohort basal area and volume response variables (PD_B, PD_MA, PD_V and PD_VG) were all significant, with r values ranging from 0.58 to 0.97. Percent difference in younger cohort plus residual basal area growth (PD_BT) was significantly correlated with younger cohort basal area and volume (PD_B and PD_V), younger cohort mean annual increment (PD_MA), and total volume (PD_VT). Although none were significant, the correlation coefficients between DF_TS and all but one other response measures were negative (Table 21).

Table 21. Pairwise Pearson correlation coefficients between response variables. Sample size was 14 in all cases.

	DF_TS[1]	PD_B	PD_BT	PD_H	PD_MA	PD_MI	PD_T	PD_V	PD_VG
DF_TS[2]									
PD_B	-0.46								
PD_BT	-0.29	0.81***							
PD_H	-0.23	0.19	0.36						
PD_MA	-0.35	0.89***	0.80***	0.28					
PD_MI	-0.09	-0.04	-0.05	0.03	0.11				
PD_T	-0.30	0.36	-0.04	-0.14	0.30	-0.46			
PD_V	-0.43	0.97***	0.85***	0.35	0.91***	0.03	0.25		
PD_VG	-0.23	0.58*	0.26	-0.08	0.66*	0.06	0.49	0.59*	
PD_VT	0.13	0.32	0.61*	0.25	0.19	-0.42	-0.15	0.32	-0.27

1--*** = p<0.001; ** = p<0.01; * = p<0.05

2--DF_TS=difference between paired plots in percent younger cohort basal area in western hemlock; PD_B=percent difference between paired plots in younger cohort basal area; PD_BT=percent difference in younger cohort plus residual basal area growth since younger cohort initiation; PD_H=percent difference in average height of younger cohort dominant and codominant trees; PD_MA=percent difference in younger cohort mean annual increment; PD_MI=percent difference in younger cohort mortality index; PD_T=percent difference in younger cohort trees per ha; PD_V=percent difference in younger cohort volume; PD_VG=percent difference in younger cohort current volume growth rate, Douglas-fir and western hemlock only; PD_VT=percent difference

in younger cohort plus residual live standing volume.

The pairs of responses and predictors selected for regression analysis (Table 22) were:

1) DF_TS and TPHI;
2) PD_B and BA_L;
3) PD_BT and BA_I;
4) PD_H and BA_I;
5) PD_MA and BA_I;
6) PD_MI and TPHI;
7) PD_T and TPHL;
8) PD_V and BA_I;
9) PD_VG and BA_L; and
10) PD_VT and TPHL.

For most of the response variables, several predictors had nearly the same degree of correlation. Thus, for many of the responses variables, alternative predictors may have been nearly as powerful.

Table 22. Pairwise Pearson correlation coefficients between predictor and response variables. Sample size = 14 in all cases. See previous tables for variable definitions.

	BA_I[1]	BA_L	CRAR	TPHI	TPHL	VOLL
DF_TS	0.40	0.50	0.36	0.60*	0.49	0.44
PD_B	-0.61*	-0.62*	-0.44	-0.55*	-0.48	-0.57*
PD_BT	-0.75**	-0.20	0.10	-0.29	-0.06	-0.16
PD_H	-0.53	-0.17	-0.05	0.00	0.15	-0.23
PD_MA	-0.76**	-0.63*	-0.34	-0.53	-0.42	-0.60*
PD_MI	-0.27	-0.29	-0.20	-0.29	-0.28	-0.26
PD_T	0.08	-0.46	-0.46	-0.36	-0.47	-0.44
PD_V	-0.71**	-0.62*	-0.40	-0.52	-0.42	-0.59*
PD_VG	-0.33	-0.67**	-0.63*	-0.59*	-0.67**	-0.64*
PD_VT	-0.04	0.48	0.51	0.38	0.53	0.48

1--** = $p<0.01$; * = $p<0.05$

Tests of effects of residual trees

Regressions of all the response variables pertaining to younger cohort basal area and volume (i.e., PD_B, PD_MA, PD_V, PD_VG) on residual basal area were significant (Table 23, Figs. 3-7). All of these response variables declined with increasing residual basal area. In all cases, the most appropriate model was curvilinear (i.e. 1/X or quadratic, Table 23); for all these models the decline in the younger cohort response was most pronounced at low levels of residual basal area (Figs. 3-7).

As judged by R^2 values, these models fit the data well (R^2

ranged from 0.63 to 0.85, Table 23). However, one influential observation was identified for both the percent difference in younger cohort basal area and percent difference in younger cohort volume models (Table 23, Figs. 3, 5). Two models were judged equally valid for percent difference in younger cohort current volume growth rate (Table 23, Figs. 6, 7). The regression of total basal area growth (younger cohort plus residual stand since initiation of younger cohort) on initial residual basal area was also significant (Table 23, Fig. 8).

To summarize the results of the regression analysis, predicted mean values and corresponding 95% confidence intervals (95%CI) were computed for all significant models, assuming initial residual basal areas of 10 m^2/ha and 17.5 m^2/ha (43.6 and 76.3 ft^2/ac)(Table 24). These levels of residual basal area represent an approximation of green tree retention levels on matrix land under the Record of Decision (USDA Forest Service and USDI Bureau of Land Management 1994), and mean initial residual basal area in this study, respectively. At 10 m^2/ha, mean percent difference in younger cohort basal area was -26% (95%CI -33% to -19%), mean percent difference in younger cohort MAI was -26% (95%CI -30% to -22%) and mean percent difference in younger cohort volume was -23% (95%CI -29% to -18%). Mean percent difference in younger cohort current volume growth rate was -22% or -17%, depending on which model was used (Table 24). Basal area growth including residual trees (PD_BT) also declined as 10

m^2/ha initial residual basal area (mean -17%, 95% CI -27% to -7%). At 17.5 m^2/ha initial residual basal area, predicted means of the younger cohort basal area and volume response variables, and PD_BT, were between -26% and -35%, with 95%CI of about plus or minus 5 to 10% (Table 24).

For most of the remaining response variables, linear regression was not significant. For PD_H, PD_MI, PD_T, and PD_VT there were no consistent trends in response to the selected residual stand measure (Figs. 10-13). DF_TS did display a pattern in relation to TPHT; however given the distribution of values it was not possible to fit a model with linear regression (Fig. 9).

Table 23. Results of tests of effects of residual trees using linear regression. Sample size was 14 for all significant models.

Response[1]	Predictor[2]	Result	Model	R^2	RMSE
DF_TS	TPHI	Linear model inappropriate			
PD_B	BA_L	$p < 0.001$ (one influential observation)	PD_B=-49.5+369.4*(1/BA_L)	0.73	12.3
PD_BT	BA_I	$p < 0.01$	PD_BT=-43.2+265.0*(1/BA_I)	0.59	17.3
PD_H	BA_I	N.S.[3]			
PD_MA	BA_I	$p < 0.001$	PD_MA=-47.4+210.2*(1/BA_I)	0.85	6.9
PD_MI	TPHI	N.S.			
PD_T	TPHL	N.S.			
PD_V	BA_I	$p < 0.001$ (one influential observation)	PD_V=-50.0+265.7*(1/BA_I)	0.83	9.3
PD_VG[4]	BA_L	$p < 0.001$ (one outlier, non-influential)	PD_VG=-42.8+320.9*(1/BA_L)	0.63	13.4
PD_VG[4]	BA_L	$p < 0.01$ (one outlier, non-influential)	PD_VG=32.6-3.97*BA_L+ 0.052*(BA_L)^2	0.64	13.8
PD_VT	TPHL	N.S.			

1--DF_TS=difference between paired plots in percent younger cohort basal area in western hemlock; PD_B=percent difference between paired plots in younger cohort basal area; PD_BT=percent difference in younger cohort plus residual basal area growth since younger cohort initiation; PD_H=percent difference in average height of younger cohort dominant and codominant trees; PD_MA=percent

difference in younger cohort MAI; PD_MI=percent difference in younger cohort mortality index; PD_T=percent difference in younger cohort trees per ha; PD_V=percent difference in younger cohort volume; PD_VG=percent difference in younger cohort current volume growth rate, Douglas-fir and western hemlock only; PD_VT=percent difference in younger cohort plus residual live volume.
2--BA_I=estimated basal area of live residual trees at initiation of younger cohort; BA_L=basal area of live residual trees; CRAR=crown area of residual trees; TPHI=estimated live residual trees per ha at initiation of younger cohort; TPHL=live residual trees per ha; VOLL=volume of live residual trees.

3--Not significant.

4--1/X and quadratic models equally valid.

Table 24. Predicted means and 95% confidence intervals for response variables with significant regression models, for 10 and 17.5 m^2 initial residual basal area/ha. See Table 23 for models.

Res-ponse	Pred-ictor	for 10 m^2/ha initial residual basal area			for 17.5 m^2/ha initial residual basal area		
		l.b. 95% CI[1]	mean	u.b. 95% CI[2]	l.b. 95% CI[1]	mean	u.b. 95% CI[2]
PD_B	BA_L[5]	-33.0	-25.8	-18.6	-38.7	-31.0	-23.3
PD_BT	BA_I	-26.9	-16.7	-6.6	-39.1	-28.1	-17.0
PD_MA	BA_I	-30.4	-26.4	-22.3	-39.8	-35.4	-30.9
PD_V	BA_I	-28.9	-23.4	-17.9	-40.7	-34.8	-28.8
PD_VG[3]	BA_L[5]	-30.1	-22.2	-14.4	-35.1	-26.8	-18.4
PD_VG[4]	BA_L[5]	-25.7	-16.7	-7.6	-35.5	-25.9	-16.3

1--Lower bound of 95% confidence interval.

2--Upper bound of 95% confidence interval.

3--1/X model.

4--Quadratic model.

5--Values corresponding to 10 and 17.5 m^2/ha BA_I calculated from linear regression models (i.e. BA_L regressed on BA_I).

The relationship between PD_MA and BA_I was still significant, but not as strong, using smaller residual plot radii (Table 25, Figs. 4, 14, 15). Among the models evaluated, the linear model was the best fit to the data for residual plot radius 24.81 m. This model had a lower R^2, and higher RMSE, than the model for residual plot radius 30.90 m. In addition, the presence of one influential outlier detracted from the fit of the model to the observations. A linear model was also the best fit to the data for residual plot radius 18.72 m. This model had markedly more scatter around the regression line (*i.e.* lower R^2) than the model for residual plot radius 30.90 m. The 1/X model could not be evaluated for either residual plot radius 24.81 m or 17.82 m because one plot lacked residual trees within the smaller radii plots.

Table 25. Linear regression of percent difference in younger cohort mean annual increment on initial residual basal area assuming smaller radii of influence of residual trees. Sample size was 14 in all cases.

Residual plot radius (m)	Result	Model	R^2	RMSE
30.90	$p < 0.001$	PD_MA=-47.4+(210.2*(1/BA_I))	0.85	6.9
24.81	$p < 0.001$ (one influential outlier)	PD_MA=-2.02-(1.39*BA_I)	0.72	9.5
18.72	$p < 0.001$ (one outlier)	PD_MA=-17.1-(0.55*BA_I)	0.31	14.9

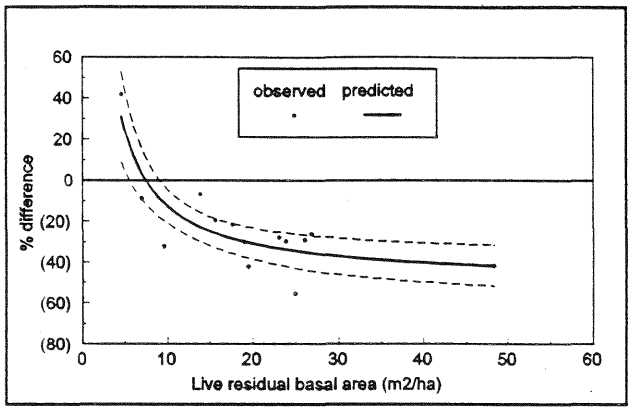

Figure 3. Plot of percent difference younger cohort basal area versus live residual basal area, with regression line (1/X transformation), and 95%CI for predicted mean response.

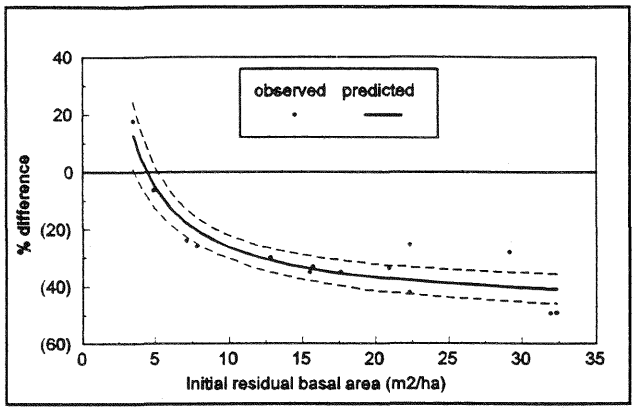

Figure 4. Plot of percent difference younger cohort mean annual increment versus initial residual basal area, with regression line (1/X transformation), and 95%CI for predicted mean response.

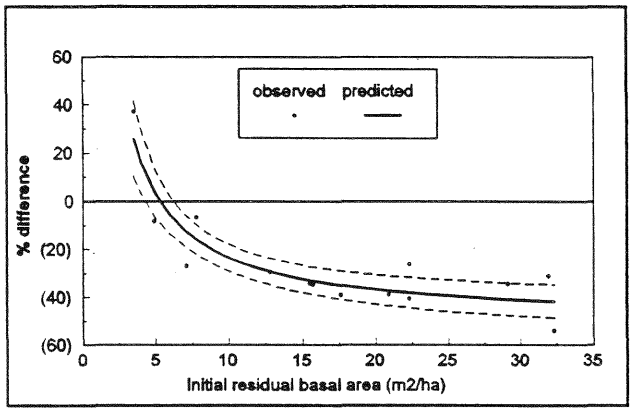

Figure 5. Plot of percent difference younger cohort volume versus initial residual basal area, with regression line (1/X transformation), and 95%CI for predicted mean response.

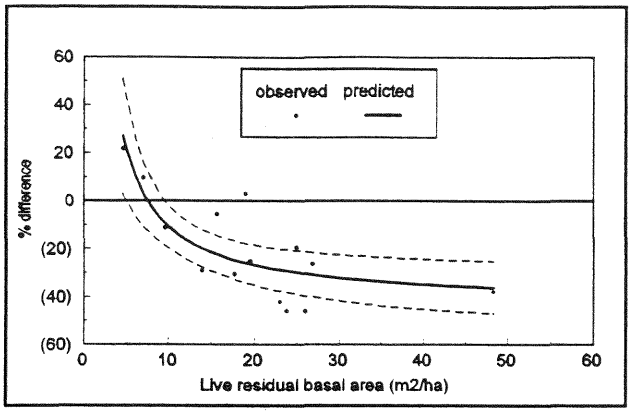

Figure 6. Plot of percent difference in younger cohort volume growth rate versus live residual basal area, with regression line (1/X transformation), and 95%CI for predicted mean response.

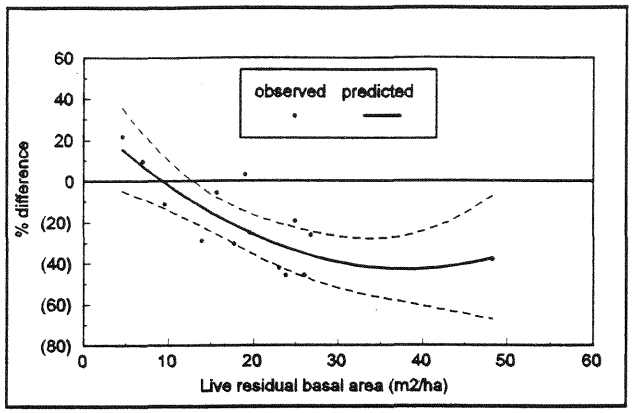

Figure 7. Plot of percent difference in younger cohort volume growth rate versus live residual basal area, with regression line (quadratic model), and 95%CI for predicted mean response.

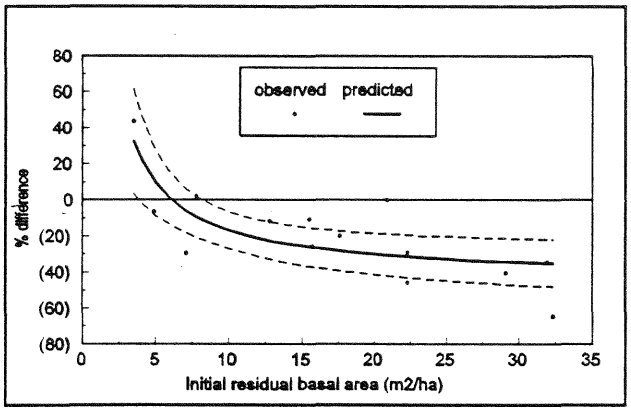

Figure 8. Plot of percent difference younger cohort plus residual basal area growth since younger cohort initiation, versus initial residual basal area. Regression line (1/X transformation) with 95%CI for predicted mean response, also plotted.

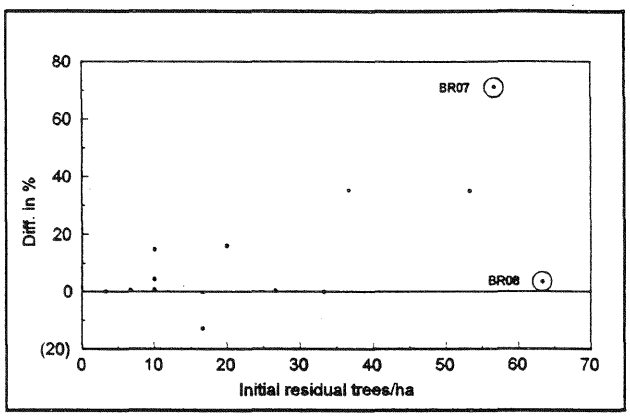

Figure 9. Plot of difference in western hemlock as percent of younger cohort basal area versus initial residual trees per ha. Observations that invalidated linear model indicated.

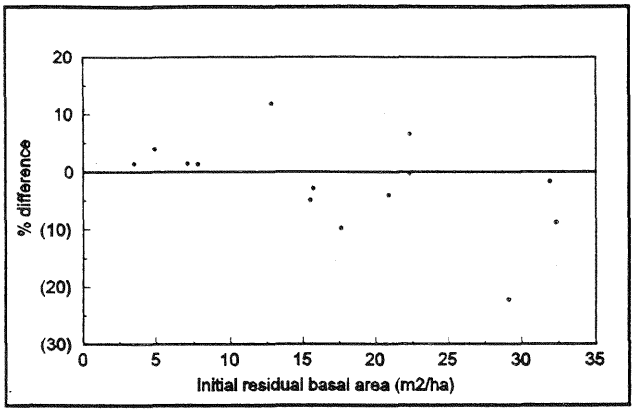

Figure 10. Plot of percent difference in average younger cohort heights (codominants and dominants) versus inital residual basal area.

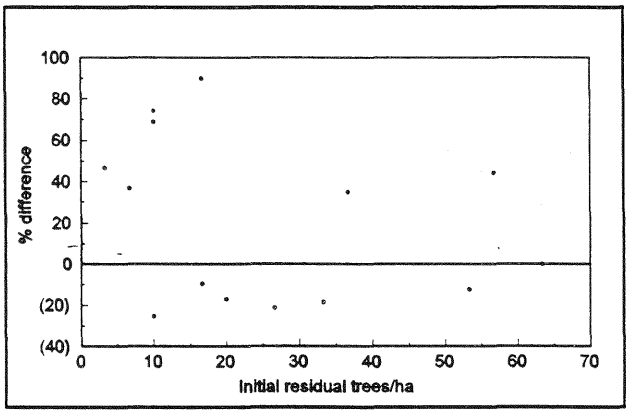

Figure 11. Plot of percent difference in younger cohort mortality index versus initial residual basal area.

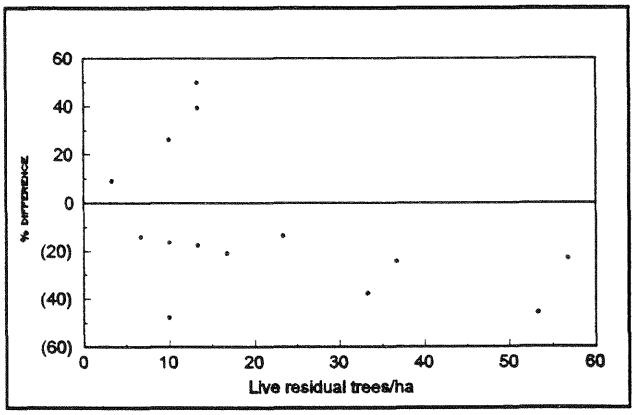

Figure 12. Plot of percent difference younger cohort trees per ha versus live residual trees per ha.

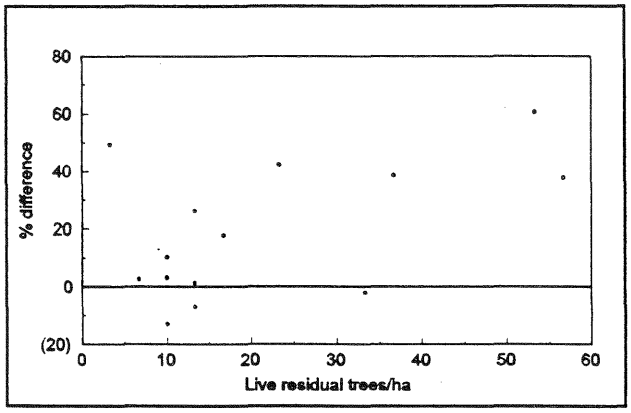

Figure 13. Plot of percent difference in younger cohort plus live residual volume versus live residual trees per ha.

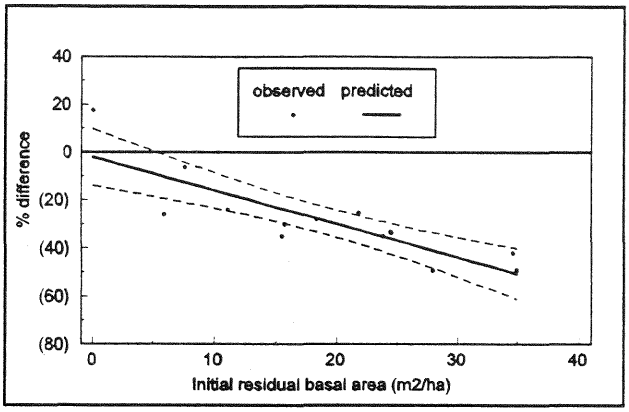

Figure 14. Plot of percent difference younger cohort mean annual increment versus initial residual basal area, using a residual plot radius of 24.81 m. Regression line with 95%CI for predicted mean response also plotted.

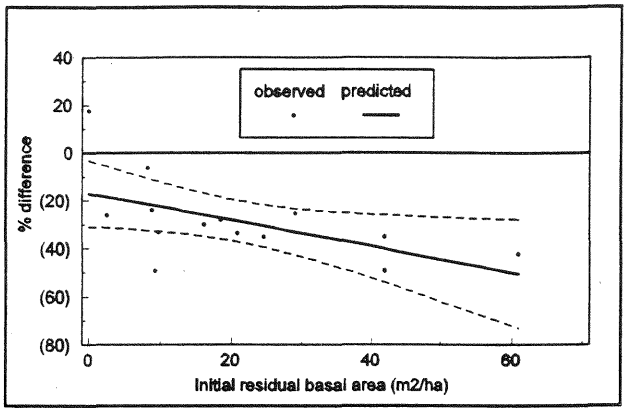

Figure 15. Plot of percent difference younger cohort mean annual increment versus initial residual basal area, using a residual plot radius of 17.82 m. Regression line with 95%CI for predicted mean response also plotted.

DISCUSSION

The set of natural, two-aged stands in this study provides a useful reference point for consideration of forest management with green tree retention. Both general information about these stands, and in particular the effects of residual trees, may be informative. Consideration of plots that were influential or extreme observations in regression analyses can yield ecological information, and illustrate some of the shortcomings of the study. It is important to consider how managed stands are likely to differ from these natural stands. Also, a critical review of assumptions underlying this retrospective study suggests some important and tractable research.

Effects of residual trees

The natural stand structures we sampled provide a precedent for management with green tree retention. Within the western hemlock zone, we located stands in which the quantity of residual trees were consistent with recent prescriptions for green tree retention on federal forests in western Oregon (*i.e.* 5 to 25 trees per ha (2 to 10 trees/ac), (Birch and Johnson 1992)). A high proportion of the residual trees in these stands had damaged tops. In plots with or without residual trees, the younger cohort often had a significant amount of western hemlock mixed with the predominant Douglas-fir. The age-range within the younger cohort was often substantial. Residual trees did have a

negative effect on MAI, standing volume, and basal area of the younger cohort, and current volume growth rate of the younger cohort. Basal area of residual trees was more strongly correlated with these younger cohort variables than were other measures of the residual component of the stands (*e.g.* trees per ha, volume). For these stands, the effect of residuals on younger cohort MAI, basal area, volume, and volume growth rate can be represented by curvilinear relationships, with the effect per unit residual basal area decreasing as residual basal area increases. Basal area growth of the total stand (residual plus younger cohort) also declined with increasing residual basal area. Residual trees did not show an effect on volume of the total stand, average height of younger cohort dominant and codominant trees, or an index of younger cohort tree mortality.

Although most of the significant regression models predicted a positive effect of very low amounts of residual basal area, the uncertainty associated with these predictions were large. We sampled few plots at low residual basal area (*i.e.* <10 m^2/ha). Partly for this reason, the 95% confidence intervals around the predictions for low residual basal area span zero (*i.e.* no effect of residual trees) in most cases. Thus, from this study little can be said concerning the effects of low levels of green tree retention. For levels of residual basal area closer to the mean for our plots (*e.g.* 17.4 m^2/ha for initial residual basal area)

confidence intervals are narrower and do not span zero.

In the Pacific silver fir zone, we found many fewer unambiguous analogues of stand structures that might be created by green tree retention. This may be due to a different disturbance regime than in the western hemlock zone, smaller area occupied than the western hemlock zone, or both.

Simulation modeling studies provide perhaps the only results for comparison to this study. Simulation experiments have been conducted to assess implications of green tree retention on sites in the western hemlock zone similar to ours, but with planting and thinning of trees similar to current management of federal forests in western Oregon (Birch and Johnson 1992, Hansen *et al.* 1995). Comparison between the simulation studies and my results are complicated by differences in predictor and response variables, and for one study, retention of trees smaller and presumably younger than the residual trees in this study (Birch and Johnson 1992). However, general trends in the simulation studies were similar to my results. Hansen *et al.* (1995) reported cumulative basal area after 240 years, with retention of 0 to 150 trees per ha from an old-growth stand, and rotation lengths of 40, 80, 120, or 240 years. For all rotation lengths, they found a substantial drop in cumulative basal area between 0 and 5 retained trees per ha, and a more gradual decline for additional increases in retention. Birch and Johnson (1992) reported net volume growth after one or two rotations with

retention of 0 to 20 trees per acre from a mature stand, using rotation lengths of 60 or 90 years. They also found the greatest decline per retained tree occurred at low retention densities.

Influential and extreme observations in regression analysis

Detailed consideration of plots identified as influential observations or outliers suggests the importance of stand history and seed dispersal. It is clear that these driving variables may vary over scales larger than our 500 m^2 plots. Thus, the relatively small plots necessary to implement the paired plot design undoubtedly introduced unexplainable variability.

Earlier initiation of the younger cohort may explain the anomalously large basal area and volume under residual trees at location MC03, an influential observation in at least two analyses (PD_B vs. BA_L, PD_V vs. BA_I). An implicit assumption of the paired plot design was that with very low residual tree densities, younger cohort attributes should be very similar with and without residual trees. Plot location MC03, which had the lowest density of residual trees, failed to conform to this expectation. It was the only pair of plots for which younger cohort basal area and volume were larger with residual trees than without. The proximal cause of the large discrepancy in basal area and volume between the paired plots is that younger cohort trees are larger on the plot with residual trees. On both plots Douglas-fir accounts for nearly all the basal area; the density

of younger cohort Douglas-fir is identical on the two plots. However, both the average and maximum Douglas-fir dbh is greater on the plot with residual trees (47 cm vs. 40 cm, 83 cm vs 63 cm). One difference between the plots that might ultimately be responsible is that the younger cohort is 14 years older on the plot with residual trees and than on the plot without residuals (see Table 9). It is important to note, however, that MC03 is not the only pair of plots with a substantially older stand under residual trees (*cf.* plots BR17 and DE06 in Table 9).

Two outliers, both with high residual tree density, precluded finding a significant relationship between percent basal area of hemlock in the younger cohort and residual tree density (see Fig. 8). In one of the pairs (BR08), relative basal area of hemlock in the younger cohort was quite high (>60%) with or without residual trees. This suggests that one or more factors (*e.g.* seed dispersal, site conditions) operate at spatial scales larger than our plot size to influence the distribution of hemlock. In the other pair (BR07), the younger cohort was very nearly 100% hemlock under the residual trees. This may be due to both site conditions favorable for hemlock regeneration (*i.e.* bottom of a steep north-facing slope, shade from residual trees) and random spatial variation in the mixture of regenerating species (W.A. McKee, personal communication).

Comparison to managed stands

The stands in this study differed from current expectations for managed stands with respect to younger cohort density, interval of tree re-establishment, and downed coarse woody debris. It is likely that the wildfires that initiated these stands had different effects on the soil than would be expected from timber harvest and related management activities. These differences complicate application of results to managed stands, and also may indicate ecologically important distinctions between natural and management processes. In addition to potential biological differences between natural and managed stands, the difference in spatial scale between this study and management activities also requires examination.

Compared to a "typical" managed Douglas-fir plantation as envisioned for the Willamette National Forest Plan (USDA Forest Service 1990; J. Mayo, personal communication), the stands in this study had quite high tree densities. Standard management includes planting of trees at about 1400 per ha (560 trees/ac), thinnings at ages 12, 47, and 67, and assumes natural mortality of about six trees/ha/decade

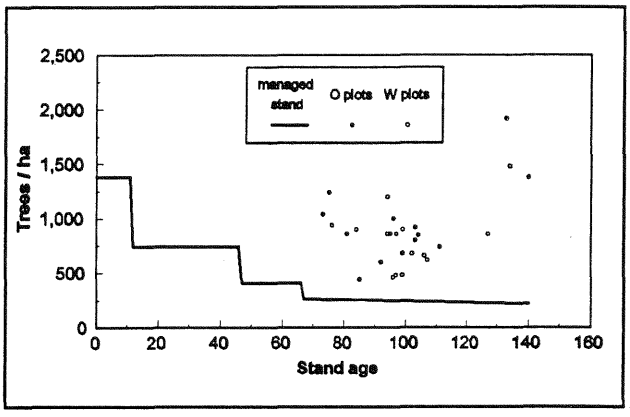

Figure 15. Comparison of younger cohort tree densities to idealized managed Douglas-fir plantation. Plots in western hemlock zone only.

thereafter (2-3 trees/ac/decade). In comparison to the tree density for a stand their age under this scenario, the stands in this study had densities between twice and seven times as high (Fig. 15). Several of the plots had densities approaching or exceeding the planting density for managed stands, at ages up to 140 years.

That the stands in this study were quite dense compared to ideal managed stands suggests that with density control it may be possible to limit the decrease in volume growth under green tree retention. To achieve tree densities one-half to one-seventh those in this study, planting and thinning could be implemented largely to avoid the immediate surroundings of retained green trees.

In contrast to contemporary legal and policy requirements for speedy regeneration of trees after timber harvest, the stands in this study exhibited a long period of tree recruitment. The Willamette National Forest Plan (USDA Forest Service 1990) requires establishment of a new tree stand within five years after harvest in most cases. In our stands, ages of cored individuals varied as much as 67 years within a plot (minimum nine years, average 28 years). It is likely that this extended period of recruitment will decrease the stand-level rate of wood volume accumulation. On the other hand, recruitment of trees over several decades may increase the diversity of tree sizes and species.

Whereas intensive management for wood production has until recently included removal of dead wood (Franklin *et al.* 1986), on average natural stands of all successional stages contain considerable amounts of downed logs and snags (Spies *et al.* 1988, Hansen *et al.* 1991). With respect to log volume, stands in this study were similar to reported values for natural young stands (average volume 242 m^3/ha (3460 ft^3/ac), range 11 to 617, see Table 9; average for natural young stands was 248 m^3/ha (3540 ft^3/ac) in Spies *et al.* 1988). Though future management of federal forests will include leaving more dead wood (*e.g.* Willamette National Forest Plan, Record of Decision), amounts may continue to be lower than averages for natural stands (*e.g.* minimum log volume prescribed by Record of Decision for Willamette and nearby National Forests is about 40 m^3/ha (570 ft^3/ac)). Decaying wood can serve as a source of organic matter and nutrients for forest soils (Harmon *et al.* 1986, Maser *et al.* 1988). However, long-term data to assess the effects of timber harvest and removal of coarse woody debris on forest productivity in the western hemlock zone apparently do not exist.

The wildfires which presumably initiated the stands in this study may have had somewhat different effects on soil than management for timber production. Since observations of intensity of the various fires are lacking, and since specifics of site and management methods determine impacts on soil, the

comparison is necessarily speculative. Wildfires may decrease surface litter and soil organic matter (Agee 1993), leading to significant losses of soil nitrogen (McNabb and Cromack 1990) and increased rates of surface erosion (Agee 1993). Timber harvest and site preparation may lead to increased soil bulk density, decreased soil organic matter, increased exposure of mineral soil, and displacement of soil (Childs *et al.* 1989). These soil changes can decrease forest productivity, for example by decreasing availability of water and nutrients, by decreasing soil aeration, and increasing resistance to root growth (Childs *et al.* 1989). Thus, the stands in this study may have developed under a different set of disturbance-imposed productivity constraints than may occur in managed stands.

Although this study quantified the younger cohort of two-aged stands within 500 m^2 plots, management activities such as green tree retention are implemented over much larger areas. Any attempts to draw inferences from this study for larger spatial scales such as cutting units must take into account several cautions.

First, application to larger scales will require some extrapolation of these results, and so is speculative. Even as speculation, application to larger spatial scales is not straightforward. Since these data are best fit by non-linear models (*i.e.* 1/X and quadratic), the predicted effect on younger

cohort basal area or volume over a larger area cannot necessarily be estimated from the mean residual basal area for an entire area. For the same overall mean values, the spatial distribution of residual trees (*i.e.* regular, random, or aggregated) will affect predictions for the younger cohort. In addition, spatial association between residual trees and younger cohort trees, either positive or negative, will affect influence of residual trees on the younger cohort. Finally, integrating predictions for the younger cohort over a larger area would require predictions for localized areas with low values of residual basal area (*e.g.* $\leq$ 5 m^2/ha (54 ft^2/ac)). However, small residual values are not well represented in this data set; one observation that was repeatedly influential in regression analyses was at the low end of residual values. Thus, dynamics of two-aged stands with relatively few residual trees remains a significant gap in knowledge.

Reconsideration of assumptions

Assumptions implicit in the retrospective approach bear reconsideration, both to emphasize limitations of this study and to point out worthwhile research questions. Especially important are assumptions concerning the disturbance that initiated the younger cohorts, the distance over which residual trees influence younger trees, and the dynamics of residual trees.

To infer that the differences between plots with and without

residual trees were due to the residual trees I had to assume that other effects of the younger-cohort initiating disturbance were not correlated with survival of residual trees. However, fire can affect all aspects of forest ecosystems, not just dominant trees (Agee 1993). The local variations in tree mortality that created the stand structures we sought may have corresponded to patterns in intensity of burning of the forest floor. Since the degree of soil disturbance can influence successional trends (Dyrness 1973, Halpern 1988), some of the patterns I observed could be due to fire effects other than tree mortality. Recent wildfires in the western hemlock zone (*e.g.* Warner Creek fire) present opportunities to test directly the degree to which canopy tree mortality is correlated with soil disturbance, and the effects of both on forest growth and succession.

To design data collection I assumed a particular, fixed radius of influence of residual trees on the younger cohort. My results suggest that the radius of influence is not much smaller than assumed (*i.e.* it is apparently not 6 m instead of 18 m, see Table 25); however it is possible that residual trees influence younger trees farther than 18 m away. More definitive answers will only be possible through long-term, manipulative experiments. Such experiments should include genetically homogeneous stock planted at prescribed distances from isolated, large trees, and encompass a variety of site types and a range of

planting densities. Less definitive, but still helpful information, could be obtained from carefully designed retrospective studies of shelterwood harvest units in which the shelterwood trees were not cut.

Some important aspects of the dynamics of the residual trees were either assumed or not addressed in this study. I assumed that the time of death of snags could be inferred from the estimated time it takes trees of different sizes to decay to different extents (*i.e.* decay classes, Maser *et al.* 1988). This is an oversimplification of the dynamics of individual trees, and may be inaccurate. I also noted that many of the residual trees had broken and/or damaged tops, and did not estimate past height growth of residual trees. Thus, I estimated basal area growth, but not volume growth, of the residual trees since younger-cohort initiation. Better understanding of timing of top damage, timing of death, and patterns of height growth of residual trees following disturbance is critical for quantifying both the effects of residual trees on younger cohort growth and other ecosystem processes, and total stand volume growth. Long-term studies of residual trees are needed, both on recent wildfires and on operational green tree retention units.

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REMNANT TREES IN RELATION TO CANOPY LICHEN COMMUNITIES IN WESTERN OREGON: A RETROSPECTIVE APPROACH

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Abstract. Trees that remain after disturbance are thought to affect stand regeneration and community development. Understanding the influences of such remnant trees on canopy lichen communities is essential for evaluating the effectiveness of the "New Forestry" practice of green-tree retention, which aims to promote biodiversity. To evaluate this impact, we sampled canopy lichen biomass in paired adjacent natural stands. Both stands in a pair had fire replacement cohorts of rotation age and one stand in each pair also had large remnant trees from the previous cohort (> 300 years old). Lichen litterfall was collected in fourteen low elevation (520 - 850 m) and four mid-elevation (1220 - 1340 m) paired stands in the western Oregon Cascades and divided into three functional groups for analysis: alectorioid lichens, cyanolichens, and green-algal foliose lichens. Although highly variable, in the low elevation stands the biomass of alectorioid lichens and cyanolichens was higher in stands with remnant trees than those without, by 132% and 30%, respectively. Alectorioid lichens were approximately five times more abundant in the mid-elevation stands than in the low elevation stands, with a median biomass of nearly 1140 kg/ha in stands with remnant trees and 700 kg/ha in stands without remnant trees. Alectorioid lichen biomass was also positively correlated with the current percentage of old forest within a 31.4 ha circle around the sampling area. Cyanolichens, which had a median biomass of 19 kg/ha (range: 0 to 255 kg/ha) in the low elevation stands with remnant trees, had a median biomass of 0 kg/ha (range: 0 to 100 kg/ha) in low elevation nonremnant tree stands. Cyanolichens were absent from all mid-elevation stands. Biomass of green-algal foliose lichens showed no differences between the low and mid-elevation stands or between the stands with and without remnant trees. Both alectorioid and green-algal foliose lichens were negatively correlated with the

density of regenerating trees.

Key phrases: green-tree retention, new forestry, ecosystem management, Pacific Northwest, lichen communities, Lobaria oregana, biomass of epiphytes, partial disturbance, Cascade Range

Key words: lichen, epiphyte, cyanolichen, alectorioid, Oregon

Introduction

Epiphytic lichens are important components in the coniferous forests of the Pacific Northwest. Alectorioid lichens provide food and habitat for wildlife (Maser et al. 1985, Rominger and Oldemeyer 1989, Servheen & Lyon 1989, Sharnoff 1994) while cyanolichens fix nitrogen (Knops et al. 1991, Pike 1978, Pike et al. 1972). Arthropods and birds utilize epiphytic lichens (Gerson and Seaward 1977, Lattin 1993; Schowalter 1988, 1995) and their diversity and abundance has been linked to epiphyte diversity (Pettersson et al. 1995).

Old-growth forests have a much higher biomass of epiphytes than even-aged, rotation-aged stands (Lesica et al. 1991, McCune 1993), and the proportion of cyanolichens and alectorioid lichens is greater in old-growth stands than in 40, 70, and even 140 year old Douglas fir and western hemlock stands (Neitlich 1993).

To improve our prediction of the likely impacts of alternative forest management practices, it is important to understand how lichen communities respond to disturbances. No data currently exist on the impacts of green-tree retention on epiphytic lichen communities. Because experiments on 80-year rotations will be slow to yield results, we have turned to studying the historical impacts of natural remnant trees on canopy lichen communities. Burns resulting in partial survival of canopy trees were common in the Pacific Northwest, as indicated by fire history studies (Morrison & Swanson 1990, Stewart 1986) and the abundance of forests composed of multiple age classes of trees. The disturbance regime changed to complete canopy removal with the popularity of clearcutting. Now, however, public forest managers in the Pacific Northwest are mandated (R.O.D. 1994) to leave 15% of the large living trees in future harvest units ("green-tree retention").

Lichens are to some unknown extent dispersal limited (Armstrong 1987, 1990, Stevenson and Enns 1992). If dispersal is strongly limiting, forests regenerating after green-tree retention cuts would be expected to have a greater lichen biomass than clearcuts due to the proximity of lichen propagule sources (assuming that lichen populations in the retention trees persisted). If, however, substrate or microclimate are more critical for determining the establishment and growth of epiphyte communities, little difference between green-tree retention cuts and clearcuts would be expected. We hypothesized that stands regenerating after green-tree retention cuts would have a greater biomass of old-growth associated lichens (e.g. Alectoria sarmentosa and Lobaria oregana) than stands without retained trees.

To examine this hypothesis we studied an analagous "natural" experiment: pairs of naturally regenerated stands, one stand with large remnant trees from a previous cohort (approximating green retention trees) and an adjacent stand without these remnant trees. Rotation-aged forests (55 to 120 years since major disturbance by fire) were chosen to provide estimates of lichen biomass in stands of an age comparable to the projected age of future harvest units. One member of each pair approximates a forest that would regenerate following clearcutting and burning. The other member of each pair approximates a forest that would regenerate after a green-tree retention cut and slash burn. This retrospective approach enabled us to evaluate the likely impacts of leaving large remnant trees through one cutting cycle without having to wait for the green-tree retention cuts of today to reach rotation age.

Methods and Materials

Stands

Eighteen stands were examined in the western Cascade Mountains of Oregon, within the Willamette National Forest. Fourteen of the stands were "low-elevation" stands (518 m to 853 m) located in the the Tsuga heterophylla Zone (Franklin and Dyrness 1973). Pseudotsuga menziesii (Mirbel) Franco and Tsuga heterophylla (Raf.) Sarg. dominated these stands and Thuja plicata Donn. and Abies amabilis (Dougl.) Forbes were often present in the understory. Four of the stands were considered "mid-elevation" stands (1219 m to 1341 m) in the Abies amabilis Zone, with Abies amabilis the dominant species.

All stands burned between 55 and 120 years ago, leaving a variable number of living remnant trees. Stands were selected so that we could sample adjacent paired plots, one with and one without remnant trees. The "nonremnant" stand had no remnant trees and was thus roughly even-aged (dominant and codominant tree ages differed less than 20 years on average; Zenner 1995). The "remnant" stand was dual-aged, with from 3 to 57 remnant trees per hectare. We sampled each stand with a 12.6 m radius "detection plot" nested within a "megaplot" of 30.9 m radius (Figure 1). Nesting the detection plot allowed for a buffer zone where remnant density was similar within and around the sampling area.

Environmental variables were recorded for each nonremnant and remnant stand. Stands were selected to keep elevation, slope, azimuth, and topographic position as similar as possible. Azimuth was adjusted to a 0-180 scale, with north and south at the poles (0 = north; 90 = east and west). Because cyanolichen abundance may vary with distance from water (Howe 1978), horizontal and vertical distance from the nearest perennial stream or

larger body of water were also recorded. Basal area of conifers and hardwoods was measured in each stand and ages were determined from increment cores (Zenner 1995).

Given the uncertainty about the effectiveness of lichen dispersal (Sillett and Neitlich 1995), we created "context" variables to evaluate the influence of remnant trees at distances greater than 30.9 m from the detection plot. These variables were created by examining recent aerial photographs (1989) of each stand and visually assigning percent cover to four categories of forest, in 3.14 ha, 31.4 ha, and 314 ha concentric circles: young (0 to 100 years), mature (100 to 250 years), old (over 250 years), and other (e.g. water, rock outcrops). These "current context" variables index the current availability of propagule sources. We also obtained earlier (1946 or 1949) aerial photographs of the stands and repeated these estimates. Due to the lower quality of the older photographs we assigned percent cover only to three categories: young (0 to 100 years), old (over 100 years), and other. These "historic context" variables index the availability of propagule sources from the surrounding landscape during approximately the first 40 years of stand development.

Litterfall Collection

Due to the impracticality of extensive direct sampling of canopy epiphytes, epiphyte biomass was estimated from collections of epiphyte litter from the forest floor. We sampled epiphytic litter in late summer to avoid the large and variable pulses of litterfall that have been recorded in winter months for some forests (Esseen 1985, Stevenson and Rochelle 1984). Because lichen litter disappears rapidly in these forests (McCune and Daly 1994), and most lichen litter falls in the winter, a single summertime sample cannot be used directly as an estimate of the annual rate of litterfall. Our data, subsequently, are not an estimation of

annual litterfall, but are used to indicate lichen biomass in the canopy.

We sampled litter in the detection plot (Figure 1) within each paired plot. A transect was laid on the contour through the center of the detection plot. From this transect, ten perpendicular transects were laid across the contour, and one 2 m radius litter plot was sampled on each of these perpendicular transects. Litter plots were placed so as not to overlap with previously sampled litter plots.

Epiphytic lichen litter (all loose litter and any present on downed branches less than 10 cm in diameter) was collected in #2 paper bags, air dried, and stored at room temperature. In the lab, samples were dried at 60°C for 24 hr and massed to the nearest milligram. Litterfall from each plot was processed separately, according to McCune (1994). Lichen litterfall was sorted into the three functional groups of McCune (1993): alectorioid lichens, cyanolichens and all remaining lichens, which are mostly green-algal foliose species. The alectorioid lichens were composed of Alectoria sarmentosa, species in the Usnea filipendula group, and several species of Bryoria (B. capillaris, B. friabilis, B. fuscescens, B. oregana, B. pseudofuscescens). The cyanolichens consisted primarily of Lobaria oregana, with small amounts of Nephroma, Pseudocyphellaria, and Sticta species. The green-algal foliose lichens were primarily Hypogymnia apinnata, H. enteromorpha, H. imshaugii, H. inactiva, Platismatia glauca, P. herrei, P. stenophylla, and Sphaerophorus globosus. Nomenclature of lichens follows Egan (1987).

Litter biomass was converted to standing epiphyte biomass based on McCune's (1994) conclusion that late-summer lichen litter in western Cascade forests in Oregon relates to standing biomass in an approximate ratio of 1:100 ($\sqrt{}$litter = 0.1 $\sqrt{}$biomass; r^2 = 0.87,

n=18). This model was based on direct sampling of epiphytes on felled trees in stands in which epiphyte litter had previously been collected (these stands were similar in elevation and species composition to those reported here). Biomass for each functional group was extrapolated to the stand level. Due to high variability among stands, the median and the range for each stand are reported instead of the mean.

Statistical Analysis

The alectorioid lichen and cyanolichen data were squareroot transformed prior to analysis to reduce skewness. A log transformation was used to improve the normality of the green-algal foliose lichen data. An arcsine squareroot tranformation was used for proportions (the current and historic context variables).

One of the 18 stands was removed from analysis after identifying several anomalous stand characteristics, the most important of which was an age discrepancy between the remnant and nonremnant tree stands. Low- and mid-elevation stands, and remnant and nonremnant tree stands, were compared on the basis of the biomass of each functional group using t-tests. Due to a significant difference in biomass between the low- and mid-elevation stands, and the low sample size of mid-elevation stands (n = 4), we report biomass for each elevation group separately (Table 1) and consider only the low-elevation stands in the analysis of the influence of remnant trees. Pearson correlation coefficients were calculated to assess the relationships between independent and dependent variables, and among independent variables.

Results

The biomass of alectorioid lichens was 140 kg/ha higher in the mid-elevation stands than in the low-elevation stands ($p = 0.015$; Table 1), while the biomass of cyanolichens was 50 kg/ha higher in the low-elevation stands than in the mid-elevation stands ($p < 0.001$). The biomass of green-algal foliose lichens was comparable among the low- and mid-elevation stands ($p = 0.115$).

Overall lichen biomass was slightly greater in the remnant tree stands than in the nonremnant tree stands (median difference = 2 kg/ha, compared with a median total biomass of 130 kg/ha in nonremnant tree stands; paired t-test, $p = 0.043$). The biomass of alectorioid lichens and cyanolichens was greater in the remnant tree stands (paired t-test, $p < 0.052$), with a median difference in biomass between the remnant and the nonremnant tree stands (remnant - nonremnant) of 41 kg/ha for alectorioid lichens and 11 kg/ha for cyanolichens. Green-algal foliose lichens did not differ between remnant and nonremnant tree stands ($p = 0.35$). Alectorioid lichen biomass was weakly related to the number of remnant trees in the megaplot ($r = 0.35$; $p = 0.08$; Table 2). Alectorioid lichen biomass was positively correlated with the 1990 percentage of old forest in a 31.4 ha area around the stand ($r = 0.47$; $p = 0.01$). Alectorioid biomass was not related to the other current or historic context variables. A negative association between alectorioid lichen biomass and the density of understory conifers ($r = -0.46$; $p = 0.02$) was also observed.

Cyanolichen biomass was greater in stands with more remnant trees than in stands with fewer remnant trees; cyanolichen biomass was positively correlated with the number of live remnants per hectare ($r = 0.50$; $p < 0.01$). Cyanolichen biomass was positively

correlated with the percentage of Tsuga heterophylla in the regeneration cohort in each stand ($r = 0.55$; $p < 0.01$). The percentage of Pseudotsuga menziesii in the regeneration cohort was negatively correlated with cyanolichen biomass ($r = -0.47$; $p = 0.01$). Cyanolichen biomass was also negatively correlated with the adjusted azimuth (-0.42; $p = 0.03$). Cyanolichen biomass was not related to the current or historic context variables.

Green-algal foliose lichen biomass was positively correlated with the basal area (m^2/ha) of understory conifers ($r = 0.52$; $p < 0.01$) and the density of understory conifers ($r = -0.73$; $p < 0.001$). Green-algal foliose lichen biomass was negatively correlated with percent slope ($r = -0.45$; $p = 0.02$). A positive correlation was seen between the 1990 percentage of clearcut forest in a 3.14 ha area around the stand ($r = 0.37$; $p = 0.04$). No relationship was seen between green algal foliose lichen biomass and any other current or historic context variable.

Discussion

Higher biomass of alectorioid lichens and cyanolichens in remnant tree stands than in nonremnant tree stands may be a function of several factors. First, some of the litterfall collected in remnant tree stands undoubtedly arose from populations in the remnant trees rather than in the regeneration. Field observations, however, suggest that lichen biomass in the young cohort was high, and clearly any litterfall in the nonremnant tree stands arose from the young cohort. Second, in the remnant tree stands the closer propagule sources may have increased the rate of population development in the young cohort. Third, although stand characteristics were comparable between the remnant and nonremnant tree stands, microclimates within the stands were probably different, historically as well as currently. In particular, scattered remnant trees may have ameliorated microclimate extremes in the early years after disturbance.

We propose three hypothesis for the influence of remnant trees and young stand development on epiphytic lichens (Figure 2). The proposed mechanisms are consistent with the observed correlation structure of our data, but require further work for confirmation.

Hypothesis 1: Nearby old-growth forests foster the development of alectorioid biomass by enhancing propagule rain. Alectorioid biomass was correlated with the percentage of old-growth forest in a 31.4 ha around each plot.

The only other observations that the landscape context is important for rebuilding epiphyte species are relatively anecdotal. Many observers have noted that cyanolichens are more abundant in the edges of young stands that adjoin old forests than in the interior of large young stands. Sampling lichen fragments on a transect from an old forest into a

clearcut revealed a negative exponential decline in the biomass of fragments moving away from the forest edge (unpublished data, B. McCune). Based upon Stevenson's (1978) report of a similar pattern with Alectoria and Bryoria fragments, Esseen et al. (in press) proposed that due to the large size of their fragments, alectorioid lichens disperse shorter distances than species that rely on soredia or other, smaller propagules. More work is required on the rates and patterns of population rebound in very large burns and clearcuts.

Hypothesis 2: Leaving remnant trees directly and indirectly increases cyanolichen biomass. Directly, remnant trees may provide canopy habitat that maintains the microclimate conditions and substrate availability necessary for the establishment and growth of Lobaria oregana and alectorioid lichens. Remnant trees maintain a source of propagules for old-growth associated species from persistent populations, which rebuild populations in the regeneration cohort at a greater rate than in stands lacking close propagule sources. Indirectly, remnant trees may shade regenerating stands and promote both old-growth associated lichens and Tsuga heterophylla. As levels of green-tree retention increased in these stands, the basal area of T. heterophylla tended to increase slightly, while that of Pseudotsuga menziesii decreased (Zenner 1995). Differences in understory vascular plants in these stands (Traut 1994) suggest that factors such as light interception, throughfall, and other microclimatic conditions were different between the remnant and nonremnant tree stands. Some of these differences may be mediated by the larger proportion of Tsuga in the remnant tree stands.

The effectiveness of remnant trees in rebuilding epiphyte populations depends on the survival of the trees and their epiphytes after the canopy is opened. There is considerable

concern that remnant trees will blow down soon after their neighbors are harvested, but it appears that in the Pacific Northwest at least some remnant trees persist for a long time (Agee 1991, Spies & Franklin 1988). Survival of the epiphytes in isolated trees has not been studied directly in the Pacific Northwest, but results from the tropics suggest that the distribution and abundance of nonvascular epiphytes will change but the old-growth associated species may persist (Sillett et al. 1995).

Hypothesis 3: Density of the regenerating cohort reduces alectorioid and other lichen biomass. Lichen growth and establishment may have been suppressed in dense stands due to decreased light and moisture penetration through the canopy.

Variation in the structure of young stands has been largely neglected as a factor controlling the rate and type of epiphyte development. However, diversity and abundance of epiphytic lichens is linked to the structural diversity of young conifer stands, in particular the presence of canopy gaps filled with hardwood trees and shrubs (Neitlich & McCune 1995). In Montana, stands having been partially opened by disease or fire often host richer epiphyte communities (McCune and Antos 1981).

In summary, our results indicate that in lower elevation stands dispersal is potentially limiting for alectorioid lichens and cyanolichens but not for the dominant green-algal foliose lichens. Dispersal of alectorioid lichens may be quite effective at the scale of individual harvest units if sufficient propagules are present. Where these propagule sources are absent, however, alectorioid lichens are less abundant.

If we assume that epiphytes respond similarly to green-tree retention cuts and to fires that result in scattered remnant trees, then our retrospective study allows us to suggest the

following: 1. The old-growth associated alectorioid lichens and species such as Lobaria oregana will be favored by leaving dominant and codominant green trees, as compared to clearcutting; 2. Populations of green-algal foliose species, particularly in the genera Hypogymnia and Plastimatia, may be relatively resilient to both clearcuts and green-tree retention cuts. These species may be more effective at dispersal and colonization than are alectorioid lichens and cyanolichens; 3. The landscape context for the disturbance may influence the rate of development of epiphyte communities in regenerating stands. In particular, an abundance of alectorioid lichens in adjoining stands may accelerate their recolonization and redevelopment in disturbed stands.

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Table 1. Median estimated biomass of epiphytes (kg/ha) in western Oregon. The range is given in parentheses.

	Single-aged stands without remnant trees (nonremnant)	Dual-aged stands with remnant trees (remnant)
Low-elevation stands (520-850 m)		
Alectorioid lichens	171 (31-439)	275 (82-803)
Cyanolichens	0 (0-100)	19 (0-255)
Green-algal foliose lichens	563 (132-1518)	450 (136-1037)
Mid-elevation stands (1220-1340 m)		
Alectorioid lichens	697 (232-1461)	1139 (156-2188)
Cyanolichens	0 (0)	0 (0)
Green-algal foliose lichens	330 (69-1161)	162 (99-619)

Table 2. Pearson correlation coefficients for lichen biomass and stand characteristics in western Oregon.

	% TSHE[1]	% PSME[2]	Density[3]	# Remnants	BA[4]	Slope	Azimuth	31.4 old[5]	3.14 clearcut[6]
Cyanolichens	0.55**	-0.48**	0.17	0.50**	-0.20	0.22	-0.42*	0.22	-0.24
Alectorioid lichens	-0.24	0.26	-0.46**	0.35*	0.29	0.03	0.19	0.47**	0.03
Green algal foliose lichens	-0.35*	0.37*	-0.73**	-0.24	0.52**	-0.45**	0.31	-0.18	0.37*
No. of Remnant trees	0.42*	-0.39*	-0.05	1.00	0.09	0.18	-0.21	0.75**	-0.18
% PSME[2]	-0.89**	1.00	-0.22	-0.39*	0.24	-0.27	0.74**	-0.28	0.11
Density[3]	0.24	-0.22	1.00	-0.05	-0.39*	0.47*	-0.33	0.09	-0.54**
Stand age	0.60*	-0.38	0.27	0.22	0.08	0.11	-0.63*	0.20	-0.01
Aspect	-0.83*	0.74**	-0.33	-0.21	0.34	-0.44*	1.00	-0.13	-0.03

1	Elevation	0.27	-0.36	0.35	0.15	-0.25	0.75**	-0.58**	0.24	-0.05
2	Water[7]	-0.28	0.07	0.05	0.05	-0.19	0.50*	0.07	0.08	-0.22
3	31.4 clearcut[8]	-0.07	0.15	-0.41*	-0.13	0.05	-0.23	-0.01	-0.50*	0.84**
4	314 old[9]	0.14	-0.13	-0.11	0.56**	0.19	0.03	0.04	0.73**	0.01

5 [1] Percentage of basal area composed of Tsuga heterophylla

6 [2] Percentage of basal area composed of Pseudotsuga menziesii

7 [3] Regeneration cohort density, trees/ha

8 [4] Regeneration cohort basal area, m2/ha

9 [5] Percentage of old growth forest in a 31.4 ha area surrounding each plot in 1990.

10 [6] Percentage of clearcut area in a 3.14 ha area surrounding each plot in 1990.

11 [7] Vertical distance to nearest perennial body of water, m

12 [8] Percentage of clearcut area in a 31.4 ha area surrounding each plot in 1990.

13 [9] Percentage of old growth foreste in a 314 ha area surrounding each plot in 1990.

14 * Two-sided p-value less than 0.05

1 ** Two-sided p-value less than 0.01

CAPTIONS

Figure 1. Sampling schematic, showing the lichen litter plots within the detection plot portion of the megaplot.

Figure 2. Proposed hypothetical relationships between the number of remnant trees, the amount of nearby old forest, regeneration density, and lichen biomass. Observed correlation coefficients are indicated. Grey lines indicate relationships not supported by observed correlations.

Fig 1

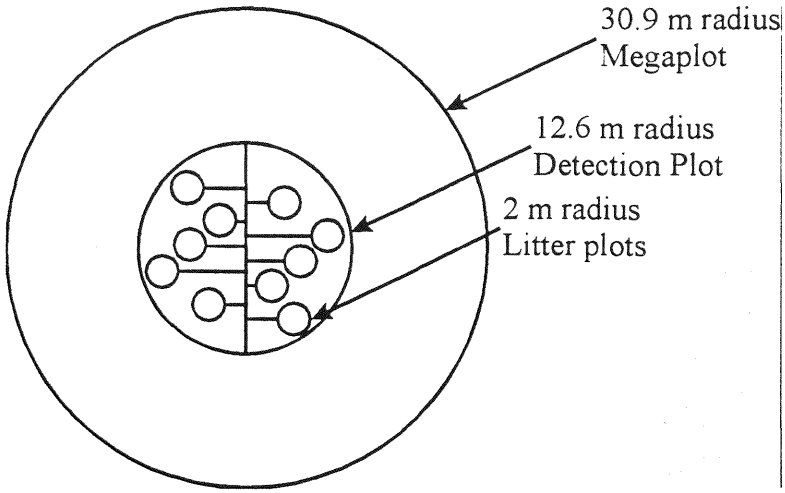
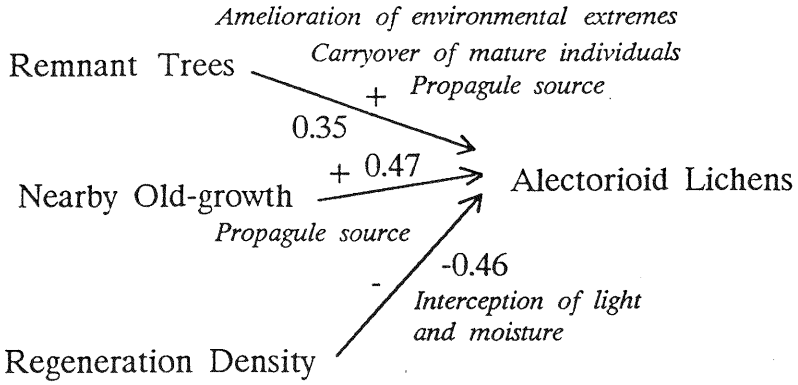
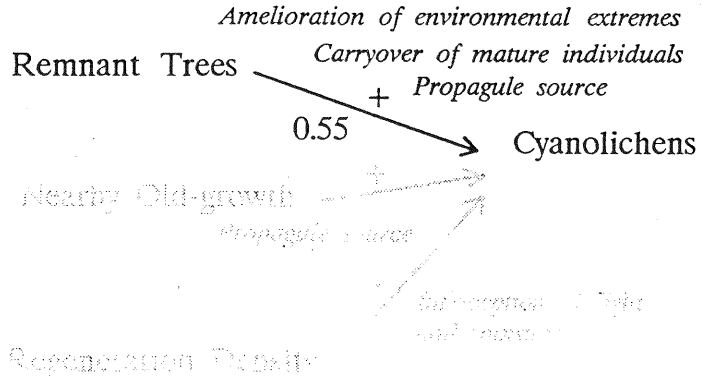
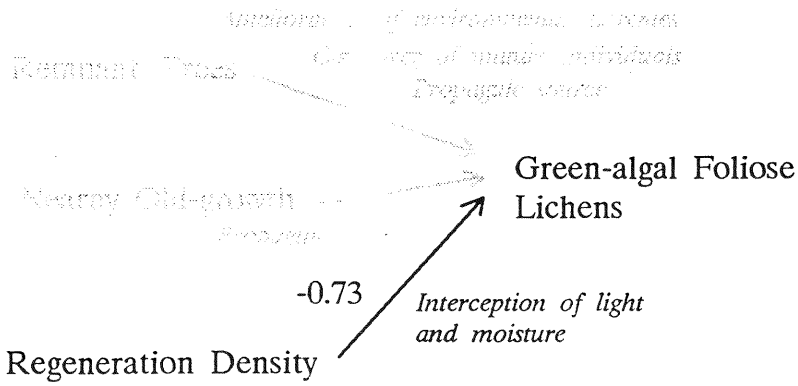

30.9 m radius
Megaplot
12.6 m radius
Detection Plot
2 m radius
Litter plots

Fig 2


Amelioration of environmental extremes
Remnant Trees
Carryover of mature individuals
Propagule source
+
0.35
+ 0.47
Nearby Old-growth
Propagule source
Alectorioid Lichens
-0.46
-
Interception of light
and moisture
Regeneration Density


Amelioration of environmental extremes
Remnant Trees
Carryover of mature individuals
Propagule source
+
0.55
Cyanolichens


Green-algal Foliose
Lichens
-0.73
Interception of light
and moisture
Regeneration Density

Effects of retained green trees on diversity and dominance of mycorrhizal types on planted Douglas-fir seedlings

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Introduction

Current changes in silvicultural thinking and practice in the Pacific Northwest emphasize the need for maintaining ecosystem integrity and biodiversity. Land managers are designing timber harvesting and reforestation techniques that will increase species and structural diversity. Green tree retention units are one example of this practice. The retained mature trees provide future structure and habitat otherwise not available in a traditional clear-cut harvest unit. The effects of leaving green trees on these harvested sites for seedling growth, future timber production and overall forest health and biodiversity, however, are unknown.

In addition to providing aboveground structure and diversity, retained green trees provide below ground structure, habitat, and rhizosphere diversity. All forest trees form mycorrhizae and mycorrhizal fungi require the living host tree for their energy source. Thus, leave trees can provide inoculum for future seedlings at the critical time of establishment. The composition of mycorrhizal fungi also changes during forest development; many fungi are adapted to conditions following disturbance (early successional fungi) while others are adapted to the stable conditions of mature forests (late successional fungi). Retained green trees may therefore maintain a compliment of late successional mycorrhizal fungi that provide important functions to the developing forest such as nutrient cycling or retention, or produce fruiting bodies as food for small mammals.

We would like to understand more about the influence of retained green trees on mycorrhizal diversity of the next generation of conifer seedlings. Douglas fir and western hemlock form mycorrhizal associations with hundreds of species of mycorrhizal fungi. These fungi differ

strongly in their benefits to their host tree and ecosystem function. For example, some fungi are more efficient at nutrient uptake while others provide drought tolerance. Still others are important in the complex forest food web. Thus, we expect that maintaining a diverse below ground population of mycorrhizae will provide developing conifers resiliency in times of nutrient or drought stress, and also facilitate ecosystem functioning.

This study was designed to examine the effect of retained green trees on the diversity and dominance of mycorrhizal types on Douglas-fir seedlings planted at increasing distance from individual green trees. This seedling bioassay for mycorrhizal types approach was chosen over sampling for fungus fruiting bodies because typically ectomycorrhizal fungi produce sporocarps sporadically during the year and in low abundance on recently disturbed sites with few remaining tree hosts. Whereas diversity of mycorrhizal types can be quantified at any time during the year without reference to identity based on fruiting bodies, and seedlings are the primary benefiting unit from fungal diversity retained on roots of live trees. We hypothesize that seedlings planted closer to retained trees will develop more mycorrhizal types or form mycorrhizae with a different guild of fungi than seedlings planted farther from the retained trees. Specific questions include: (1) Is diversity of mycorrhizal types greater near retained trees than further into the cut-over site? (2) Does nearness to trees affect the fungal composition and dominance of specific mycorrhizal types?

Methods

Study areas

Three study sites were located in the McKenzie Ranger District within Ambush Units 4, 5 and 6 at an elevation of 2600 feet. Aspect of the units were south, southeast, and southwest respectively. Size varied between 10-20 acres with 2-4 green trees/acre. Canopies of various green trees had fire damage. Study units were logged during the fall of 1992 and broadcast burned in May 1993. Douglas fir seedlings, 2-0 from J. Herbert Stone Nursery, were used in this study.

Planting and excavation of seedlings.

Ten seedlings were planted 1.5 meters apart on each of four radial transects beginning at 1.5 meters from tree out to 15 meters. Preliminary examination of seedling roots showed some mycorrhizal colonization from the nursery. Planting was completed in early June 1993.

A total of one hundred and seventeen Douglas fir seedlings were excavated in July 1994 as follows: Unit 4, ten seedlings from one transect each for two trees (A and B). Unit 5, seven to ten seedlings from one transect each for five trees (C, D, E, F, and G). Unit 6, nine to ten seedlings from two transects for one tree (H); nine to ten seedlings from one transect each for four trees (I, J ,K , and L).

Seedlings were placed in plastic bags, returned to the laboratory and refrigerated until root systems could be examined.

Mycorrhizal assessment.

Soil was removed from the root systems by overnight soaking and gentle washing. Two sub samples, 5 cm apart, of 2.5 cm bands across the root system were examined under a dissecting microscope for each seedling. Well developed mycorrhizal tips were placed in small vials for further description of microscopic characteristics as well as for microphotographs.

The numbers of mycorrhiza types were recorded for each root system sub sample. The number of mycorrhizal root tips for each type was counted and abundance calculated as percentage of total mycorrhizal root tips sampled for each seedling.

Statistical Analyses

Regression correlations and analysis of variance ($p<0.05$) were performed for total number of mycorrhizal tips and mycorrhizal types in relation to distance from retained trees on each site and for all sites combined.

Results

Overall mycorrhizal type diversity

Descriptions for all mycorrhizal types are given in the Appendix. A total of 43 mycorrhizal types was observed on seedlings from all sites with 11, 22, and 31 types from Units 4, 5, and 6 respectively (Table 1). Differences between sites reflect the higher number of retained trees sampled and total seedlings analyzed on sites 4 and 6 (i.e. the greater number of seedlings examined, the more mycorrhizal types recovered).

Total number of mycorrhizal types recovered along the transect per retained tree ranged from 15 on one tree to a low of 4 on two trees. For individual sites, mean number of mycorrhizal types per retained tree were similar and ranged from 7.4 to 9.8 types; with all sites combined, individual trees averaged 8.8 types (Table 1). Individual seedlings over all sites averaged 3 mycorrhizal types, and for individual retained trees mean number of mycorrhizal types per seedling ranged from1.1 to 4.1 (Table 1).

Frequency and abundance of mycorrhizal types

Figures 1-4 show the frequency of occurrence and percentage colonization for each mycorrhizal type on each site and for all sites combined. The most striking pattern is the high frequency of types 2 and 3 on all sites, averaging 94 and 82% frequency respectively. Type two was identified as *Rhizopogon* and type 3 as *Cenococcum,* both well known and common mycorrhizal fungi of Douglas-fir. *Rhizopogon* was also consistently a dominant component on all root systems, averaging 45% feeder root colonization. In contrast, although *Cenococcum* occurred at high frequency, its percentage colonization was low, typically 10%. The remaining mycorrhizal types were low in frequency, 10% or less over all sites, with 29 types occurring on 5 or less seedlings. Although most types occurred with low frequency, they often showed intermediate (20-40%) to high (50-70%) colonization on individual seedlings. Type 15, for example, had the highest colonization at 75 %.

Individual sites showed the same pattern of frequency of occurrence and colonization. *Rhizopogon* and *Cenococcum* were present on nearly all seedlings and at high and low abundance

respectively. On Unit 4, Type 1 showed high frequency and moderate abundance, but was rare on the other two sites. Unit 5 had several minor types with high abundance; and Unit 6 had several types with moderate frequency and abundance. The three sites shared many types in common, yet 3 types remained unique to Unit 4, 8 unique to Unit 5, and 12 unique to Unit 6. The higher number of unique types for Units 5 and 6 again likely reflects the increased sampling size compared to Unit 4.

Effects of distance from retained tree on mycorrhizal type frequency and diversity

Because the majority of mycorrhizal types occurred on less than 10 seedlings over all sites, we present frequency data only for the most commonly encountered mycorrhizal types over all sites (Fig.5). The two dominant types, *Rhizopogon* and *Cenococcum*, were remarkably even in frequency distribution across all distances, maintaining constant high frequencies . The remaining 5 most common types, although much less frequently encountered than *Rhizopogon* and *Cenococcum*, were also present at most distances and with fairly even distribution across distances.

Figures 6 and 7 indicate the mean number of mycorrhizal types (i.e. diversity) and Figure 8 the mean total mycorrhizal tips per seedling as a function of distance from retained trees. With all sites combined (Fig. 6), there is a decreasing trend with distance from the tree, from a high of 4.6 mycorrhiza types closest to the retained tree to a low of 2.7 types at 12m distance. For individual sites (Fig. 7), the same trends were apparent, particular for Units 5 and 6 because they showed the highest number of mycorrhizal types on seedlings closest to the retained tree. Over all sites, total mycorrhizal tips showed a similar trend of highest values closest to the tree (Fig. 8). However, because of high variation, analysis of variance and regression correlations were not significant for any of these variables.

Discussion

The primary objective of this study was to examine the effect of retained green trees on mycorrhizal diversity, abundance, and dominance of fungal types on planted seedlings. We hypothesized that mycorrhizal fungus species still in association with retained trees, and operating within the root zone of the retained trees, would develop mycorrhizae with seedlings planted into that active root zone, thereby influencing mycorrhizal development on seedlings compared to seedlings planted distantly from the retained trees where there was less or no live tree root influence, i.e. no live vegetative mycorrhizal mycelium. We assumed that mycorrhizal development on seedlings planted into soil with no active mycorrhizal fungi attached to live trees would originate from fungal propagules (spores, sclerotia, hyphal fragments) remaining in the soil after disturbance or dispersing onto the site from adjacent forests.

Although we found trends of higher mycorrhizal tip abundance and diversity of mycorrhizal types on seedlings grown close versus far from the retained trees, these differences were not significant. Therefore we must reject the hypothesis within the bounds of the experimental design that closeness to trees increases mycorrhizal diversity or dominance by certain fungal types. We believe that this finding results from two major factors. First, mycorrhizal fungus colonies are scattered and patchy in distribution around the trees, thereby reducing chances that individual seedlings will be planted into those patches to potentially retrieve active mycorrhizal types. Increased sampling size (more transects and seedlings sampled per retained tree) is needed to capture this spatial variation. Secondly, even with retained trees, the sites were severely disturbed by the logging activities, including the immediate vicinity surrounded retained trees. Such disturbance is likely operating on both macro scales (over the entire site) and micro scale (in micro niche soil habitats within the root zone). Thus, disturbance adapted fungi could outcompete late successional fungi still associated with retained trees. This latter possibility is born out by the dominance (both frequency and abundance) on all seedlings regardless of distance from retained trees by *Rhizopogon* and *Cenococcum* . Both fungi are the most commonly cited of mycorrhizal fungi found on wild or bioassay Douglas-fir seedlings planted into disturbed soils (Pilz and Perry 1983, Roth and Berch 1991, Molina et al. 1994).

Many mycorrhizal types were common to all sites. We suspect that most of the species in common are those responding to disturbance and thus early successional species. Each site also had unique mycorrhizal types but it remains unknown whether they are originating from the retained trees (late successional fungi) or simply from random distribution on the landscape.

Most seedling bioassay studies of mycorrhizal inoculum potential in disturbed forest soils remove soil from treated sites, place the soil in pots in the greenhouse, grow seedlings in the soils, and measure mycorrhizal diversity and abundance recovered on the seedlings. We chose to do a field bioassay *in vivo* so that we could directly measure the influence of active mycorrhizae of retained trees. Two other studies in the Pacific Northwest have examined mycorrhizal diversity on Douglas-fir seedlings planted onto harvested sites. Pilz and Perry (1983) recovered 11 mycorrhizal types on 3 sites in the Oregon Cascades (Willamette NF, Sweet Home Ranger District); each site included clearcut and adjacent undisturbed forest. Roth and Berch (1991) found 33 mycorrhizal types on Douglas-fir seedlings planted on 8 clearcut sites on eastern Vancouver Island, Canada. In our study of 3 green tree retention sites, we found a total of 43 mycorrhizal types. Whether this higher number of recovered mycorrhizal types on our sites is due to the presence of retained trees is uncertain because of the difficulty in comparing different sites and precision in identifying specific mycorrhizal types. However, because many mycorrhizal fungi respond to disturbance (early successional fungi) while others occur at later periods of stable forest conditions (late successional fungi), we believe that the green tree retention units provide a combination of both fungal successional groups. Many disturbance fungi are activated by the harvest activity and some late successional fungi are maintained on retained tree roots, thereby yielding the higher overall diversity on our green tree retention units compared to the clearcut units of the other two studies.

In order to more effectively address the question of the effects of retained trees on mycorrhizal diversity, several additional approaches would be helpful in future studies. First is acquiring a better understanding of the root and mycorrhizal zone of influence for the retained trees. This would require root excavation or soil coring to determine root extension as well as characterizing the specific mycorrhizal types associated with those roots. Seedlings could then be planted into known root zones; when seedlings are harvested, a representative core of nearby

"mother roots" could also be sampled so that root analysis of both seedling and core would reveal sharing of mycorrhizal types. Molecular DNA markers of the specific fungi found on those roots could also be used to support visual identification of shared mycorrhizal types. This effort would provide strong evidence of the influence of retained tree roots on mycorrhizal development on seedlings compared to areas further distant from the trees and beyond the root zone. Secondly, greater emphasis is needed on more intensively sampling individual retained trees (several transects of planted seedlings per retained tree) rather than several trees scattered over different units. Such a sampling scheme is needed to deal with the highly variable and patchy distribution of fungi in soil. Thirdly, fungus diversity, both sporocarp and mycorrhiza types, should be sampled around specified leave trees prior to unit harvest so that residual fungus species around leave trees post harvest could be directly assessed.

Conclusions

Our original objective was to evaluate whether retained green trees would maintain mycorrhizal fungus diversity on harvested sites. We chose an *in vivo* bioassay with Douglas-fir seedlings planted along radial transects from retained tree centers to test the hypothesis that seedlings planted closer to the tree, and thus in the active root and mycorrhiza zone of the retained tree, would form more mycorrhizal types or have their root systems dominated by different mycorrhizal fungi than those seedlings grown farther from the retained trees and outside the root zone of influence. Our results failed to support that hypothesis. We believe this was due to a combination of the patchy nature of mycorrhizal colonies surrounding the retained trees, high variation of mycorrhizal development on seedlings, small sampling size, and the large scale disturbance surrounding retained trees that stimulated activity of early successional mycorrhizal fungi adapted to disturbance.

Overall mycorrhizal diversity on the three sites combined, however, was high; we recorded 43 mycorrhizal types. Two other relevant field bioassays of clearcut sites (Pilz and Perry 1983, Roth and Berch 1991) found 11 and 33 mycorrhizal types on planted Douglas-fir seedlings. We

suspect that the higher total mycorrhizal diversity seen in this study was due a combination of activation of early successional, disturbance adapted mycorrhizal fungi, and the presence of active mycorrhizal fungi maintained by the retained green trees. Future study in this area must include measurement of the active root/mycorrhiza zone of the leave trees, assessment of the mycorrhizal types on the leave trees, and larger sampling designs of seedlings planted into known active and nonactive root zones of the leave trees. Studies should also be of longer duration.

References

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Pilz, D. P. and D. A. Perry. 1983. Impact of clearcutting and slash burning on ectomycorrhizal associations of Douglas-fir seedlings. Can J. For. Res. 14: 94-100.

Roth, A. L. and S. M. Berch. 1991. Ectomycorrhizae of Douglas-fir and western hemlock seedlings outplanted on eastern Vancouver Island. Can. J. For. Res. 22: 1646-1655.

Appendix -- Description of mycorrhizal morphotypes (photographs are available from the authors)

Morphotype 1

Brown. Reddish brown in KOH under compound microscope. Non-branched. Emanating hyphae lacking. Thin mantle. Inner mantle a net synenchyma. Hyaline to slightly colored hyphae, 4-6 μm in diam. Clamp connections present.

Morphotype 2

Rhizopogon vinicolor. Whitish and brown mycelium in the outer mantle. Thick outer mantle. Distinctive inner mantle of very compacted hyaline hyphae. Rhizomorphs well developed of brown hyphae.

Morphotype 3

Cenococcum geophilum. Dark brown. Thick-walled brown emanating hyphae.

Morphotype 4

Pale cream brown. Not well developed. Thin mantle of about 25 μm. Orange-brown under compound microscope. Outer mantle is a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 5

Pale brown translucent mantle. Mantle up to 50 μm thick. Outer mantle of thin-walled hyaline hyphae. Regular synenchyma. Orange-brown under compound microscope. No clamps connections or rhizomorphs were observed.

Morphotype 6

Pale cream brown. Outer mantle up to 50 μm thick. Net prosenchyma of hyaline hyphae. Orange brown to olive brown under compound microscope. Ventricose cells or cystidia present in

the outer mantle. Inner mantle a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 7

Brown with dark spots. Mantle up to 25 μm thick. Outer mantle of thick-walled brown hyphae. Net synenchyma. Reddish-brown under compound microscope. Scattered long emanating hyphae. No clamp connections or rhizomorphs were observed.

Morphotype 8

Brown. Slightly pinnate or branched. Thin mantle of brown thin-walled hyphae 4-8 μm forming a net prosenchyma. No clamps or rhizomorphs were observed.

Morphotype 9

Olive. Mantle up to 50μm thick. Outer mantle of hyaline to olive hyphae, 2-4 μm diam forming a net prosenchyma. Abundant clamp connections. No cystidia present. Inner mantle of irregular interlocking synenchyma. Few and very compacted rhizomorphs.

Morphotype 10

Brown. Felty aspect. Mantle up to 75 μm thick. Outer mantle of thick-walled brown hyphae, 2-5 μm diam forming an irregular synenchyma. Brown and short emanating hyphae present. Clamp connections present. No rhizomorphs were observed. Inner mantle a net synenchyma.

Morphotype 11

Green. Pinnate. Mantle up to 40 μm thick. Outer mantle of thick-walled brown hyphae, 2-4 μm diam. Clamp connections present. Inner mantle a net synenchyma.

Morphotype 12

Pale brown. Long tips. Mantle up to 50 μm thick. Orange-brown under compound microscope. Outer mantle of hyaline to pale olive forming a net prosenchyma. Abundant cystidia, 45 x 5 μm. Inner mantle a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 13

Yellowish. Swollen aspect. Mantle up to 40 μm thick. Outer mantle of hyaline to brownish hyphae forming a net prosenchyma. Yellowish to olive under compound microscope. Inner mantle a net synenchyma. Clamp connections and rhizomorphs present.

Morphotype 14

Orangish brown. Pinnate. Mantle up to 50 μm thick. Outer mantle of hyaline to olive hyphae 2-4 μm diam forming a net prosenchyma. Inner mantle of an irregular synenchyma. Abundant clamp connections in outer surface. Rhizomorphs were not observed.

Morphotype 15

Brown and translucent mycelium. Mantle up to 40 μm thick. Felt prosenchyma of hyaline, thin-walled hyphae, 2-4 μm diam. Abundant clamp connections. Inner mantle a synenchyma. Rhizomorphs of grayish color present

Morphotype 16

Brown. Swollen aspect. Mantle up to 75 μm thick. Outer mantle of thick-walled brown hyphae, 2-4 μm diam forming an stellate pattern. Emanating hyphae and clamp connections present in the outer surface. Setae or cystidia present up to 50 μm long.

Morphotype 17

Rusty brown. Mantle up to 40 μm thick. Outer mantle of thick-walled brown hyphae, 2-3 μm diam forming a felt prosenchyma. Rhizomorphs present. Clamp connections were not observed.

Morphotype 18

Blackish brown. Mantle up to 40 μm thick. Outer mantle of a stellate to regular synenchyma. External brown hyphae, 2-4 μm diam. thick walled originating from the stellate cells. Inner mantle a net synenchyma. Brown rhizomorphs present. Clamp connections were not observed.

Morphotype 19

Peach color. Mantle up to 50 μm thick. Pale cream color under compound microscope. Outer mantle of hyaline hyphae forming a net prosenchyma. Inner mantle of a net synenchyma. Outer surface hyphae branching profusely resembling basidia. No clamps or rhizomorphs were observed.

Morphotype 20

Rusty yellow-brown. Mantle up to 60 μm thick. Outer mantle of thin-walled olive-brown hyphae forming a net prosenchyma. Inner mantle of a net synenchyma. Clamp connections present. No rhizomorphs were observed.

Morphotype 21

Golden cream. Pinnate. Mantle up to 60 μm thick. Outer mantle of a net prosenchyma. Abundant external hyphae of thick-walled, hyaline to olive hyphae, 2-4 μm. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 22

Green. Outer mantle of a net prosenchyma. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 23

Yellowish. Mantle up to 50 μm thick. Outer mantle of a net prosenchyma. Short emanating hyphae, cystidia-like, 5 μm diam, hyaline. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 24

White translucent. Orange brown under compound microscope. Outer mantle of a felt prosenchyma, difficult to distinguish the thickness. Hyaline hyphae, 2-3 μm abundant on the outer surface. No clamp connections or rhizomorphs were observed.

Morphotype 25

Pale rusty brown to brown. Branched. Mantle 25-40 μm thick. Outer mantle of a net prosenchyma. Abundant emanating hyphae, hyaline to slightly colored, 2-5 μm diam. Clamp connections present in emanating hyphae. Inner mantle of a net synenchyma. No rhizomorphs were observed.

Morphotype 26

White translucent. Pale olive under compound microscope. Mantle up to 75 μm thick. Outer mantle of a net prosenchyma. Inner mantle of a net synenchyma. No clamps connections or rhizomorphs were observed.

Morphotype 27

Golden. Mantle 25-50 μm thick. Distinctive emanating hyaline to pale olive brown, 2-4 μm. Outer mantle of a felt prosenchyma. Inner mantle of a net synenchyma. No clamps connections seen.

Morphotype 28

White grayish. Compact aspect. Mantle up to 50 μm. Brown under compound microscope. Short emanating hyaline hyphae up to 5 μm in diam. Outer mantle of a net

prosenchyma. Inner mantle of a net synenchyma. Clamp connections present. No rhizomorphs were observed.

Morphotype 29

Brown. Resembles old mycorrhizae tips. Inner mantle of thick-walled, dark septate hyphae. No clamp connections or rhizomorphs were observed.

Morphotype 30

Olive yellowish. Thin-walled, hyaline hyphae, 2-5 μm in diam. in the outer surface. Outer mantle of a net prosenchyma. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 31

Orange brown. Emanating tapered hyphae (setae) up to 150 μm long, 2-4 μm in diam. Outer mantle of an irregular synenchyma (no interlocking). Inner mantle of an irregular synenchyma (interlock). No clamp connections or rhizomorphs were observed.

Morphotype 32

Dark brown. Felty appearance. Short emanating, thick-walled hyphae, 2-3 μm in diam. Outer mantle of a regular synenchyma (stellate). Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were seen.

Morphotype 33

Pale brown. Brown to orange brown under compound microscope. Patches of white mycelium on mantle. External hyaline to slightly brown, 2-5 um in diam. hyphae. Mantle 50 μm thick. Outer mantle of a net prosenchyma. Distinctive cells up to 25 μm in diam in cross section. Inner mantle of a net synenchyma. Clamp connections and rhizomorphs were observed.

Morphotype 34

Brown. Thin mantle. External thin-walled, bluish-green hyphae, 2-3 μm in diam. Outer mantle of a net prosenchyma. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 35

Grayish brown. Mantle 50 μm thick. Brown to dark brown in cross section under compound microscope. Outer mantle of thick-walled, olive to brown hyphae, 2-5 μm in diam forming a net prosenchyma. Emanating hyphae present. Inner mantle of a net synenchyma. Clamp connections present. No rhizomorphs were observed.

Morphotype 36

Orangish. Mantle up to 25 μm thick. Distinctive outer layer of cellular appearance in cross section. Cells up to 20 μm in diam. Outer mantle of a regular synenchyma. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 37

Pale brown. Mantle up to 50 μm thick. External hyaline to pale olive hyphae in cross section under compound microscope. Outer mantle of a net prosenchyma. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 38

Dark brown. Mantle up to 75 μm thick. External thick-walled, dark brown cells, up to 65 μm in diam in cross section. Emanating hyphae, 5-8 μm in diam. Outer mantle of a regular synenchyma. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 39

Pale brown. Swollen aspect. Mantle up to 100 μm thick. Pale olive laticiferous hyphae, up to 5 μm in diam. Outer mantle of a felt prosenchyma. Inner mantle of a net synenchyma.

Morphotype 40

Pale brown. Slender and short tips. Mantle up to 15 μm in diam. External thin-walled, pale olive to hyaline hyphae. Outer mantle of net prosenchyma. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 41

Reddish brown. Mantle up to 25 μm thick. Outer mantle of a thick-walled, brown hyphae forming a net prosenchyma. Inner mantle of a net synenchyma. No clamp connections or rhizomorphs were observed.

Morphotype 42

Orangish brown. Thin mantle of thin-walled, olive to brown hyphae. Outer mantle of a net prosenchyma not well developed. Inner mantle of a net synenchyma.

Morphotype 43

Pale brown. Olive under compound microscope. Mantle up to 65 μm thick. Emanating thin-walled, hyaline to pale olive hyphae, 2-5 μm in diam. Clamp connections present. No rhizomorphs were observed.

TABLE 1. Total and mean number of mycorrhizal types on seedlings planted on the green tree retention units.

Unit	4		5					6					
Tree	A	B	C	D	E	F	G	H_1	H_2	I	J	K	L
Total number of types/tree	9	9	4	11	8	8	6	5	13	12	15	4	10
Mean number of types/seedling	2.8	3.4	1.1	3.4	2.7	2.3	2.5	2.4	4	5	4.1	1.6	3.2
Mean number of types/tree/unit	9		7.4					9.8					
Total number of types/unit	11		22					31					

Fig. 1. Percentage frequency of mycorrhizal types and mean mycorrhizal colonization on seedlings from all units combined

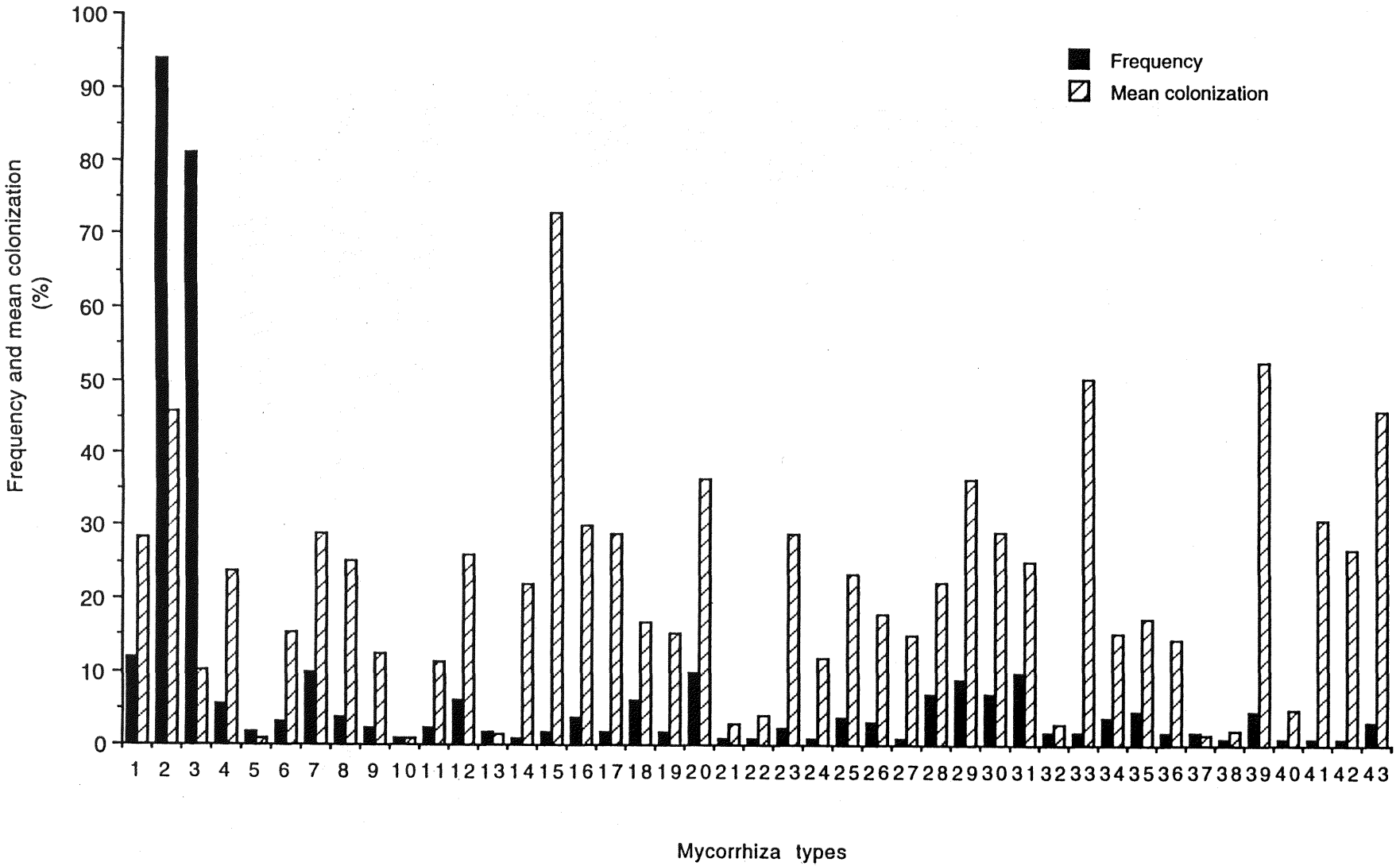


Fig. 2. Percentage frequency of mycorrhizal types and mean mycorrhizal colonization on seedlings in Unit 4

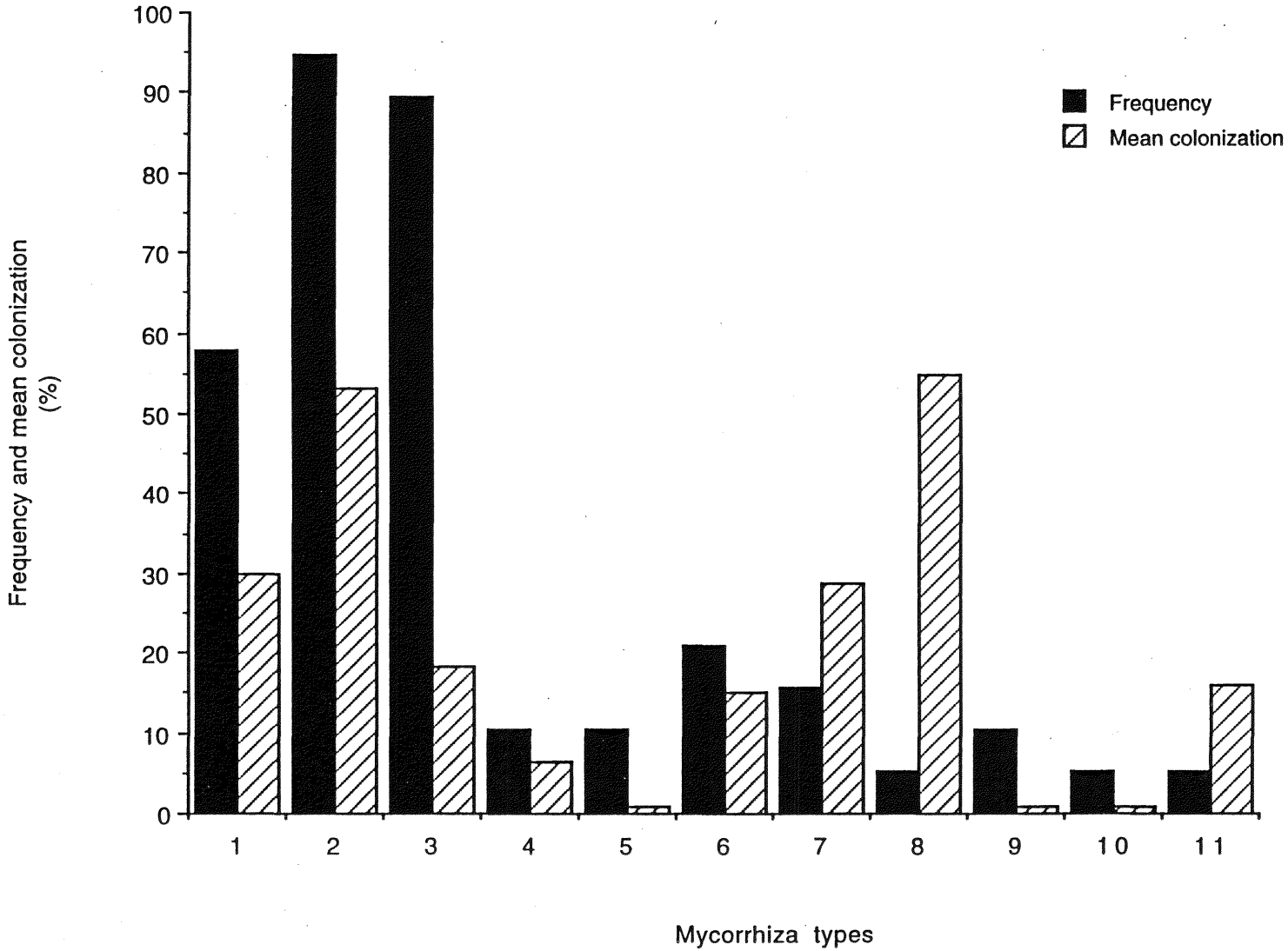


Fig. 3. Percentage frequency of mycorrhizal types and mean mycorrhizal colonization on seedlings in Unit 5

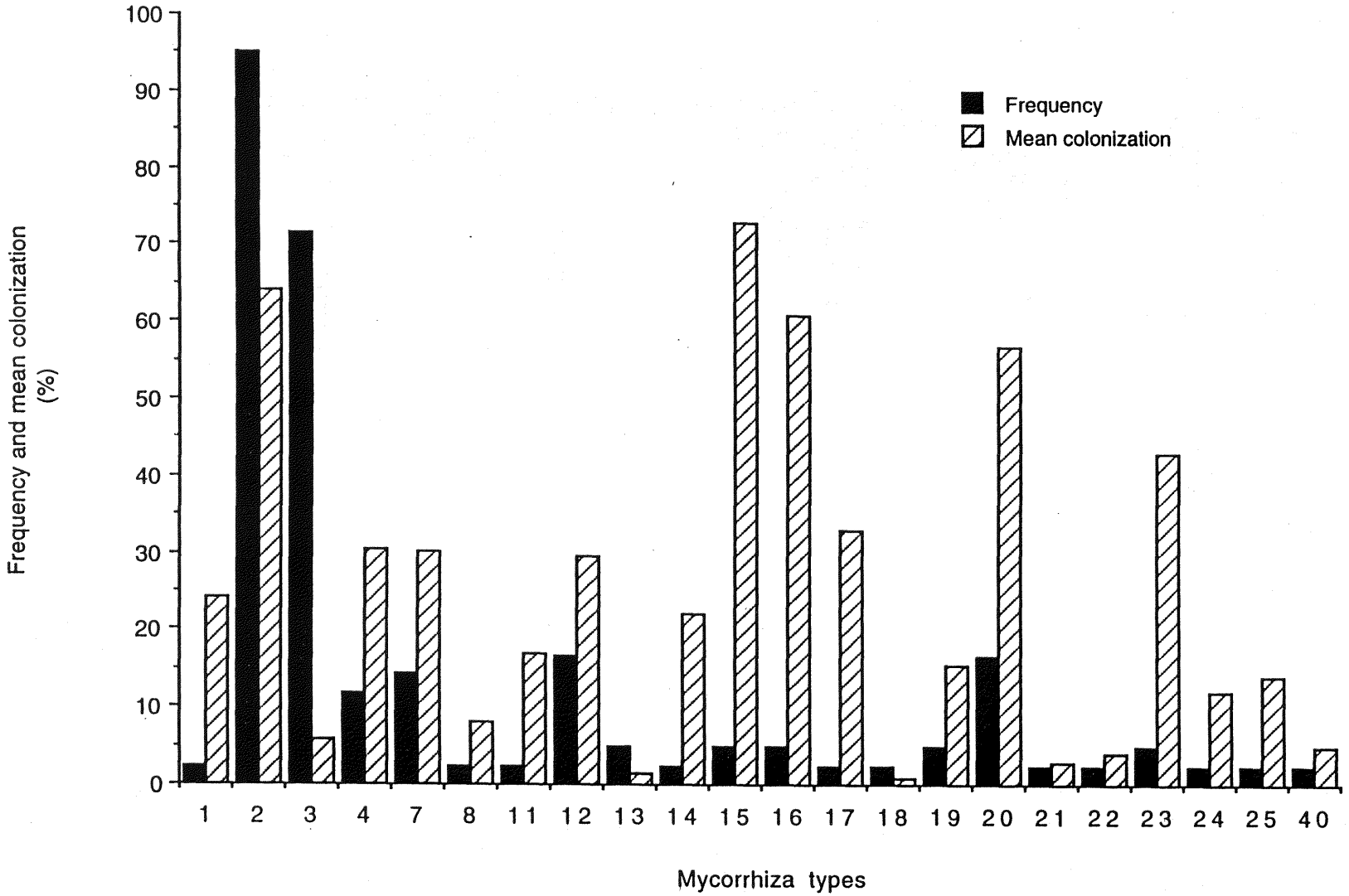


Fig. 4. Percentage frequency of mycorrhizal types and mean mycorrhizal colonization on seedlings of Unit 6

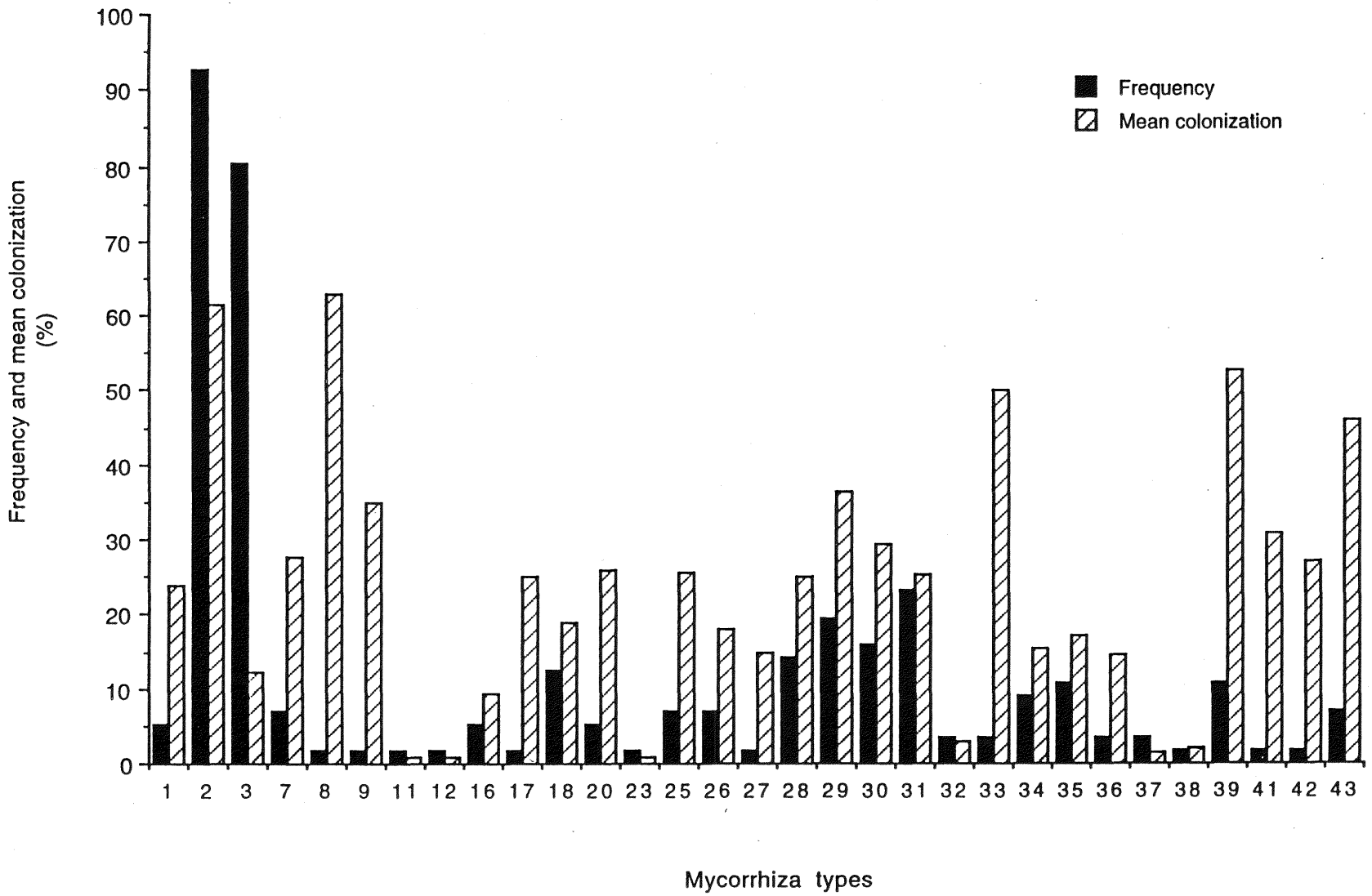


Fig. 5. Percentage frequency of the seven most common mycorrhizal types on all seedlings from all units

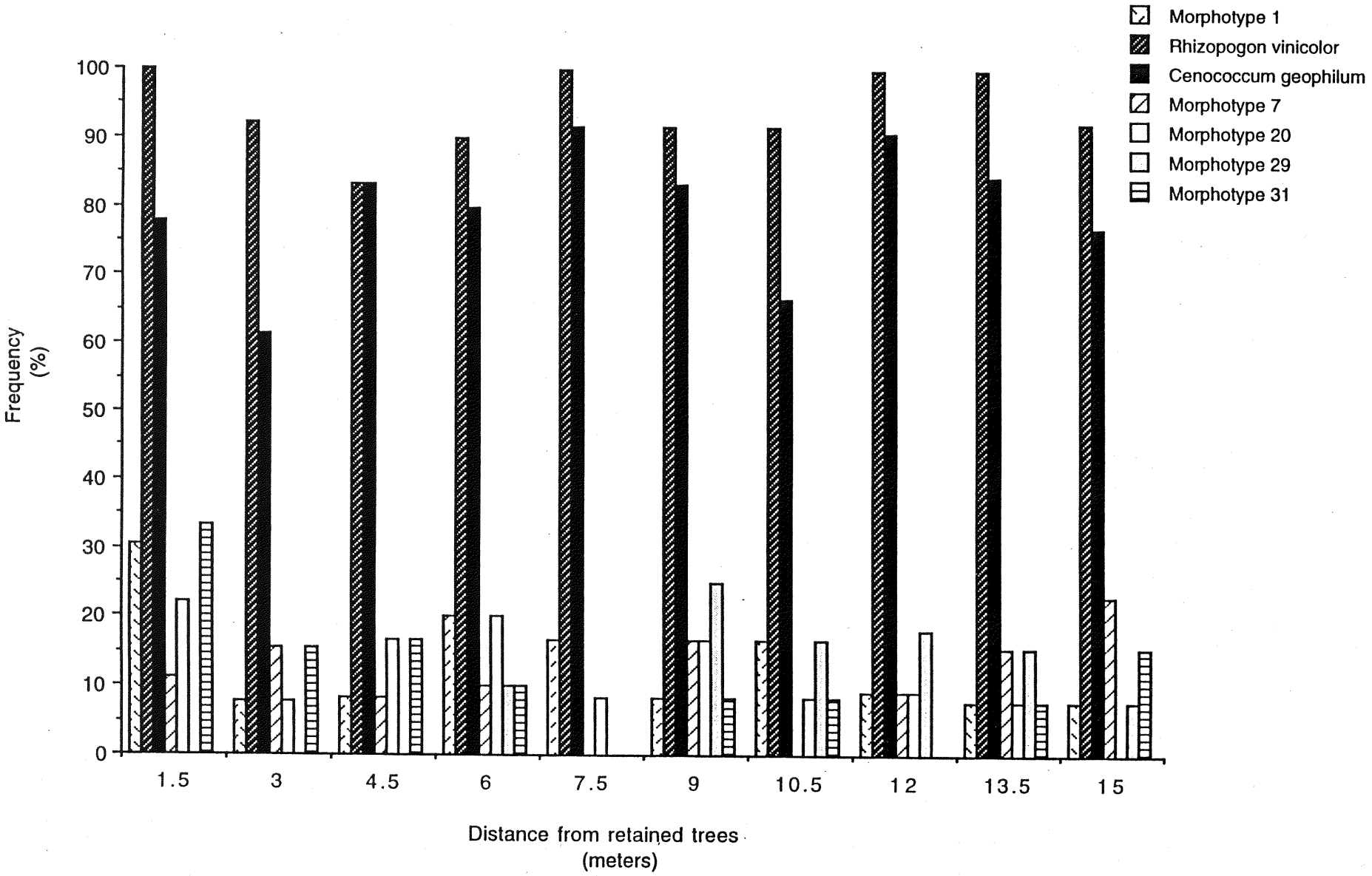


Fig. 6. Mean number of mycorrhizal types in relation to distance from retained trees for all units combined (Bars denote std. deviation)

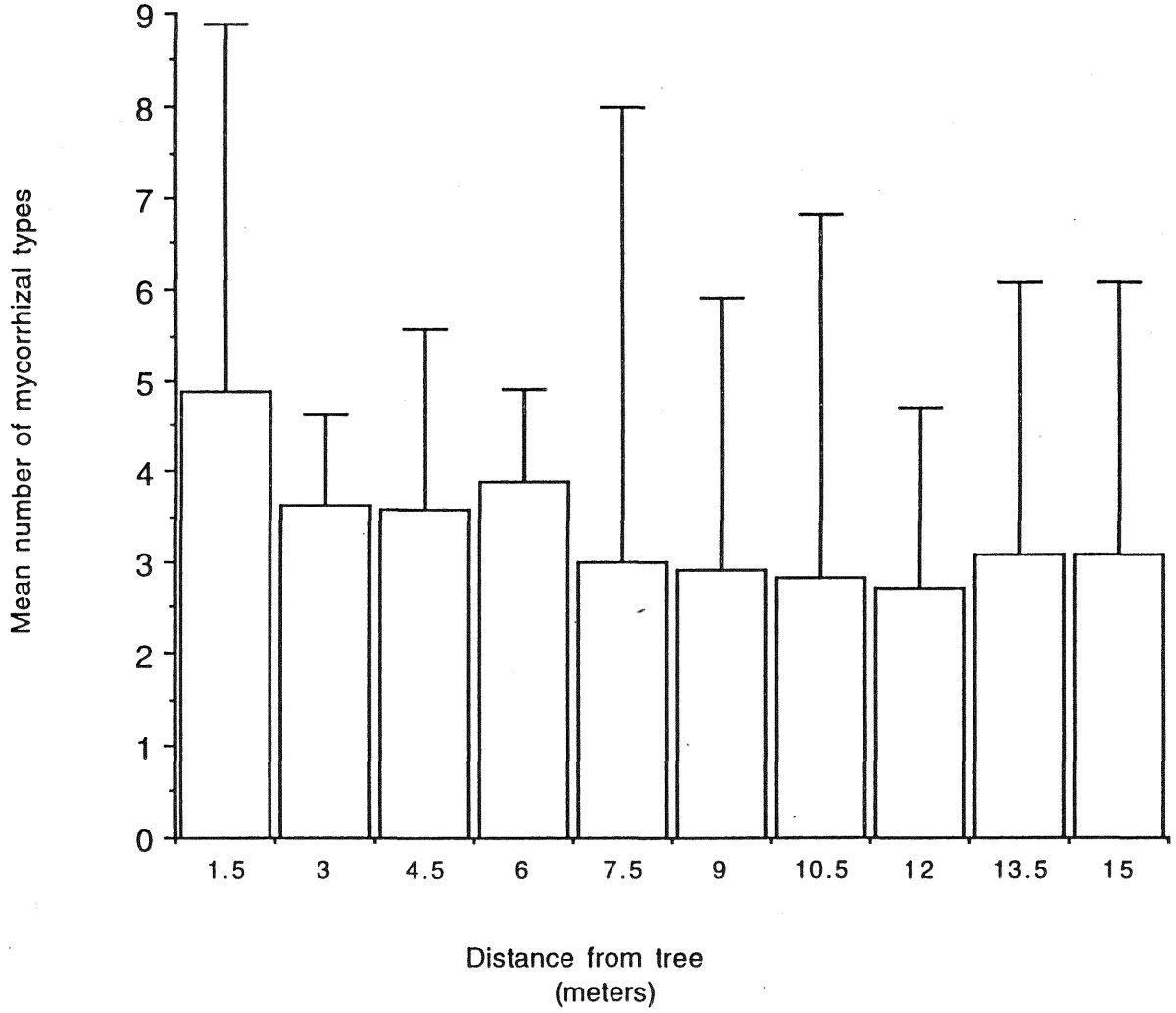


Fig. 7. Mean number of mycorrhizal types in relation to distance from retained trees for individual units

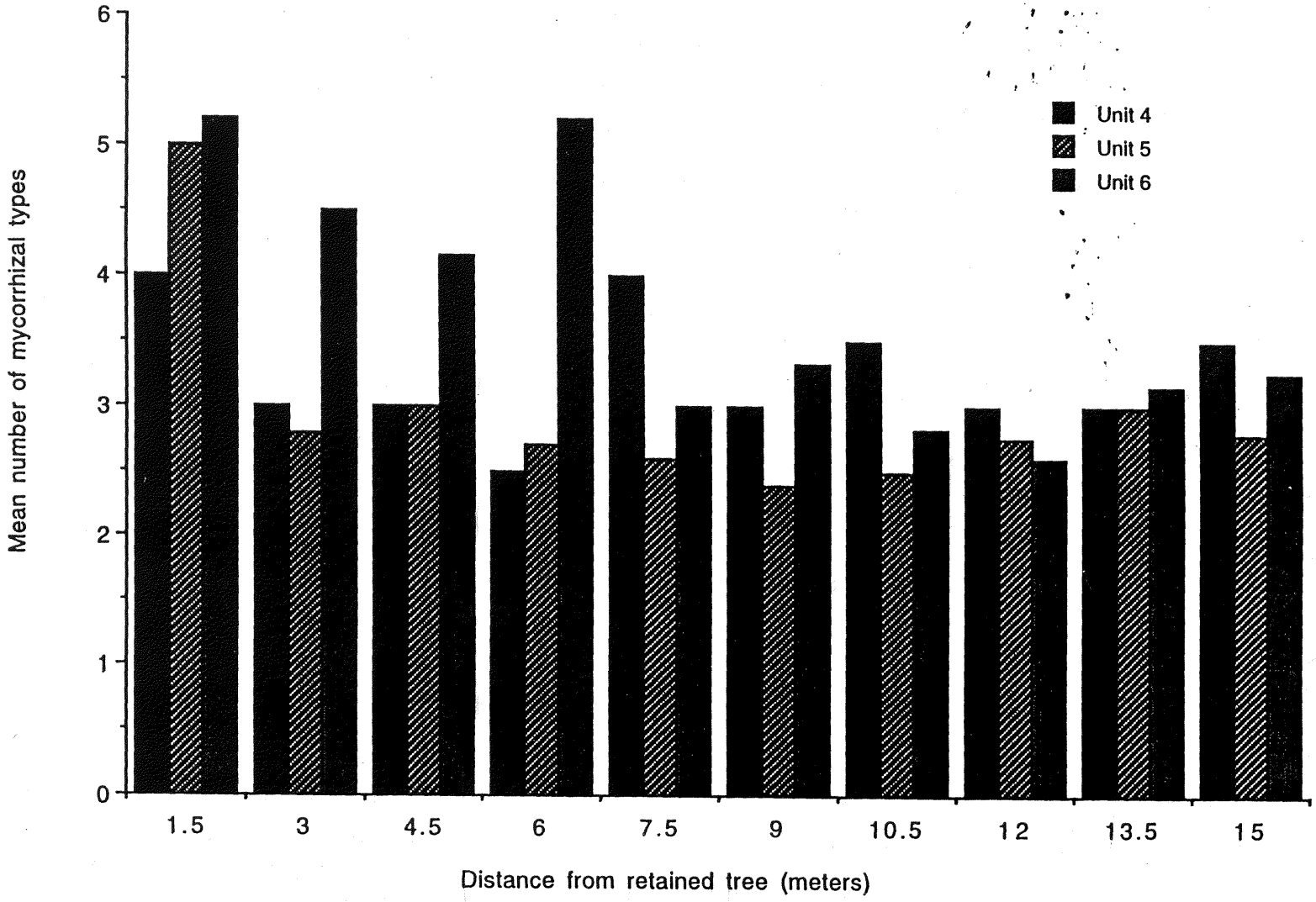
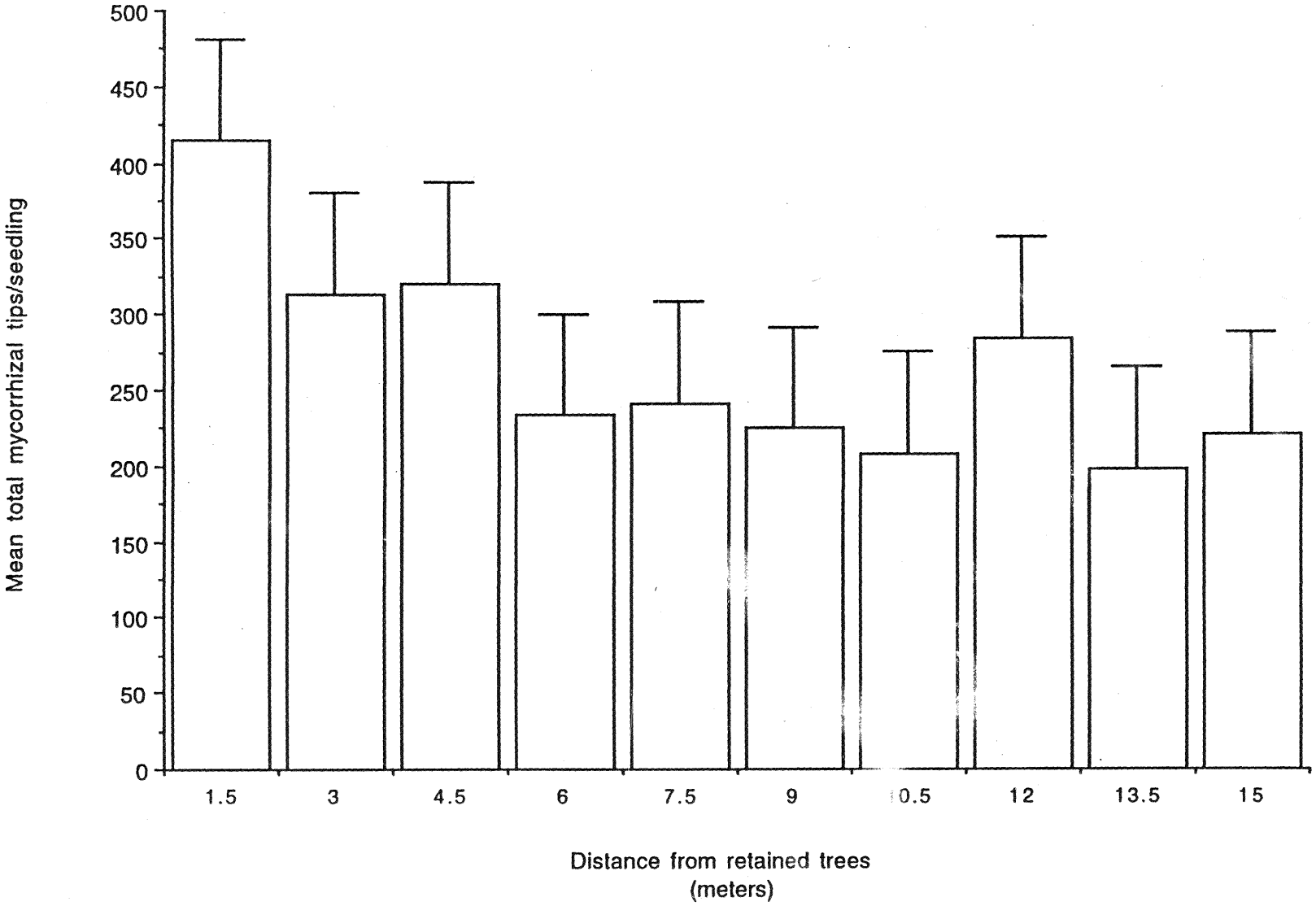


Fig. 8. Mean total mycorrhizal tips/seedling as a function of distance from retained tree for all sites combined (Bars denote standard errors)



Arthropod abundance, biomass and diversity as a function of forest management type

A.R. Moldenke

INTRODUCTION

Though an interesting ecological feature in its own right, the diversity and abundance of insects and their relatives has far-reaching consequences throughout the food web of a forest community. Ecologists, forest managers, the lumber industry and the general public are generally agreed upon the benefits of maximizing biodiversity within forest stands. Points of disagreement arise over the cost of managing for biodiversity, and whether or not organisms without the support of public interest groups (i.e., bugs, fungi) need to be included within such concerns. Once even the staunchest opposition is made aware of the myriad critical functional roles these overlooked members of the forest community play, support *in theory* for maintaining their levels of natural diversity is usually forthcoming. The science of maintaining their diversity, and the effort required, remain minimally understood subjects.

This study was undertaken: (1) to show that biodiversity of arthropods may be estimated in several practical methodological approaches, with contrasting approaches revealing information useful on different spatial and temporal scales; (2) to show that abundance, biomass and diversity are not always correlated in nature; and (3) to establish linkages between the arthropod fauna and other more well-studied faunal elements (i.e., birds, mammals, reptiles).

Arthropods are marvelously fascinating to entomologists in their own right, but on an ecosystem scale they are critical to other elements in terms of the processes they regulate (i.e., pollination of plants, rate of decay and consequent nutrient recycling), and the obvious reality that they themselves represent an exploitable food resource. I will demonstrate that the levels of arthropods available as potential food items varies by several orders of magnitude between contrasting stages of forest succession and contrasting forest management scenarios. Since this is an introductory inventory of the arthropod fauna, I will postulate without proof that such differences in biomass availability cannot fail but have indirect controlling influences on vertebrate abundance and diversity.

Clear-cutting (usually accompanied by subsequent broadcast burning of slash) has been the standard method of harvest in the Oregon Cascade Range. This management procedure removes all of the overstory and most of the understory (all the remaining understory is usually consumed by the subsequent site preparation burning). The plant community developing in a clearcut is structurally simple and without a canopy. Mature second generation forests in this region are dominated by Douglas-fir (*Pseudotsuga menziesii*), and usually are characterized by an understory of western hemlock (*Tsuga heterophylla*) saplings. An additional shrub layer may or may not be present.

METHODS

Pitfall trapping: Two parallel 75m transects, 25m apart, were installed in each study site. Two pitfall traps (Moldenke, 1994) were sunk into the ground surface with an intervening perpendicular distance of 1m, every 25m interval along the transect (N = 6 x 2 = 12). Every trap was comprised of an approximately 1l plastic food cannister, within which an 8 oz cup was set under an aluminum funnel (upper edge flush with diameter of 1l container (diameter = x 15cm); lower edge with a hole 3 cm wide to prevent vertebrates from becoming entrapped). Each cup was filled to a depth of 5cm with a 50:50 mixture of ethylene glycol:water as a non-volatile preservative. Traps were harvested after an interval of 21 days.

Beating/sweeping: At each pitfall trap site, a circular area 5m in diameter was sampled by beating and/or sweeping (N = 6). Beating shrub branches (between 0.3-2.5m in height) was the predominant form of collecting in the forest understory, whereas sweeping all vegetation was the dominant method in the clearcuts. Each method was utilized when appropriate to sample all the vegetation within the 5m radius circular area. Arthropods collected by each method were aspirated into vials in the field and preserved in 50% ethanol.

Sticky traps: Five meters perpendicular to the transect line (displaced so as not to affect the other sampling methods) a 1.0m tall by 0.5m wide wire mesh of 0.8mm "hardware cloth" was stapled to an erect wooden pole driven into the ground (N = 6). The

perforated mesh was covered with Tanglefoot@, an extremely sticky adhesive, to which flying insects adhered upon contact. The top of the active collecting surface was placed 2m above the ground surface. Adjacent branches which might contact the sticky mesh when moved by the breeze, were removed.

Soil cores: A rectangular core (25cm x 25 cm x 8cm deep) was removed at each pitfall position and placed into a ziplock plastic bag (N = 12). The contents were placed into Tullgren extractors at Oregon State University, and the extracted fauna identified under a dissecting microscope.

Site selection: Two low-elevation sites representing clearcuts, mature forest and green tree retention were chosen in the vicinity of the Andrews Experimental Forest, Willamette National Forest, Lane County, Oregon (approximately 75km east of Eugene). Precise study sites are mapped in Hansen et al. (1995).

Since this was an exploratory study, I attempted to include sites representing the maximum degree of variability within each category. One of the clearcut sites was severely broadcast-burned during site preparation for replanting; as a consequence the ground cover was a very dense cover of largely introduced herbaceous annual species. The other clearcut was only patchily burned and supported a significant component of resprouting native perennial species. Of the two green tree retention sites, one was only lightly burned while the other was severely burned with similar effects on the regenerating flora. The two mature

forests also differed in the understory vegetation: the vegetation of one site was a monoculture of *Gaultheria shallon*, while the other was diverse and multilayered.

RESULTS

Pitfall trapping

The mobile arthropod community living on the ground surface is far more numerous in clearcut than green tree retention (GTR), and more numerous in GTR than mature forest (Table 1); each respective comparison decreases approximately 50%. The major components of clearcut are ants (34%) and beetles (24%); those of GTR are ants (24%), spiders (13%) and millipedes (17%); mature forest is characterized by even mixes of beetles, millipedes, camel-crickets and spiders (each 20%). Ants, beetles and bugs showed great disparity between the two clearcut sites; ants (e.g., *Camponotus modoc*, *Formica* 2 spp) in preponderance at the site with shrubby regrowth; beetles (e.g., *Amara* sp, *Calosoma tepidum*) and Hemiptera (e.g., Lygaeidae) at the herbaceous regrowth site. In the GTR sites millipedes (e.g., spirobolids) were in preponderance at the unburned site, whereas Hemiptera (e.g., Lygaeidae) dominated at the burned site. The two representative forest communities had nearly identical composite group profiles.

Diurnally active species comprised approximately half of the arthropods of each community type, hence the same relationship of clear-cut > GTR > mature forest still holds true (Table 2). Though forest-dwelling ants (i.e., *Camponotus modoc*) are

diurnally active, much of this foraging takes place arboreally in the canopy and they are seldom found in large numbers in pitfall traps. Nearly all forest beetles and Orthoptera are nocturnal.

Arthropod biomass totals are driven largely by a single large inedible (Moldenke 1990) millipede species (i.e, *Harpaphe haydeniana* -- Table 1). Including *Harpaphe* in the totals, clear-cut and GTR are approximately equal in biomass and twice the amount in the mature forest. Several species of nocturnal carabid beetles similarly comprise more than 50% of the community biomass. Since *Harpaphe* is potentially active and subject to avian predation 24 hours a day, the total diurnally available biomass follows the pattern for *Harpaphe* alone -- GTR is 2-fold clear-cut, which is two fold mature forest. Excluding *Harpaphe*, the diurnally available arthropod biomass in clear-cut = GTR is 10-fold that of mature forest. The major items of arthropod biomass in clearcut are grasshoppers (28%), beetles (22%), caterpillars (18%), spiders (14%) and ants (10%). In GTR the major groups are the same but ranked respectively: Orthoptera > spiders > beetles > ants > caterpillars. In the forest, spiders (59%) and caterpillars (29%) comprise nearly all the diurnally available biomass.

Species richness increases one and one-half-fold from mature forest to GTR and an additional one and one-half-fold to clear-cut (Table 3). Forty-seven species were collected more than ten times each; 111 less frequently (N = 24 traps/community type). Seventy-four percent of the common species inhabited both clear-cut and GTR (47% of these found additionally in mature forest as

well). Only 17% of the common species were restricted to only one community type (4 in clear-cut; 4 in mature forest). Eighty-one percent of the rarer species were found in the clear-cut and/or GTR (Appendix 1).

The biomass of the epigeic arthropod food resource is comprised in large part of only 13 species: ants - *Camponotus modoc*, *Formica* 2 spp; predaceous beetles - *Calosoma tepidum*, *Pterostichus lama*, *P. herculeanus*, *P. amethystinus*; millipede - *Harpaphe haydeniana*; grasshopper - *Trimerotropis* 2 spp.; *Pristoceuthophilus celatus*; spiders - *Antrodiaetus spp*, *Cybaeus reticulatus*, *Pardosa mackenziana*. *Amara* sp.(ground-beetle), *Megalonotus sabulicola* (Hemiptera: Lygaeidae), and *Leuronychus parvulus* (skunk-spider) were the only species comprising more than 2% of the total individual census that are not main contributants to community food biomass as well (e.g., small body size).

Beating/sweeping

There is no significant difference in the total numbers of arthropods beaten and/or swept within the three community types; point site variability is very high (Table 4). In the sequence clear-cut, to GTR to mature forest beetles remain a steady 10% of the total, Hemiptera decrease from 53% to 6%, while spiders increase from 8% to 35%.

In all communities the distribution of abundances within size classes is logarithmic, 50-80% fall within the two smallest categories at each site regardless of community type. The second

forested site differs significantly from all the other five in having a significant number of larger insects (i.e., caterpillars - Table 4). The predominant groups in the smallest size category are: clear-cut = immature Hemiptera; mature forest = Psocoptera, Diptera, Collembola and spiders.

Species richness did not vary between community types, though component taxa exhibited offsetting trends (highest Hemiptera richness in clear-cut; highest spider richness in mature forest - Table 5). Total species richness of the three groups selected for further identification was about 55, slightly higher in GTR and slightly less in mature forest (mature forest richness is 71% of GTR richness). Fifty-three species were collected more than 10 times apiece, 67 less frequently. Sixty-eight percent of the common species inhabited both clear-cut and GTR (34% of these in additionally in mature forest as well). Thirty-eight percent of the common species were restricted to a single community type (8 in clear-cut, 5 in GTR, 7 in mature forest). An even number of rare taxa were found in each community type. The habitat choice of all of the commonest taxa is presented in Appendix 1.

Sticky traps

Traps in GTR collected significantly more insects than those in clear-cut, which in turn collected significantly more than those in mature forest (Table 7A). Considering only beetles, GTR has three-fold more flying insects than either clear-cut or mature forest. The majority of beetles in the clear-cut are

predominantly diurnal, while the preponderance in both the GTR and mature forest are nocturnal (Table 7B).

The distribution of size classes is logarithmic at all six sites (Table 7A). 81-99% of all flying insects comprise the two smallest categories. Both mature forest sites are characterized by larger-sized (>15mm) flying insects (e.g., beetles, parasitic wasps, moths - Table 7A); 15% are larger than 10 mm in length (< 1-3% in clear-cut and GTR). The predominant group in the smallest size category at all 6 sites is the Diptera.

Species richness is greatest in GTR, 146% higher than either clear-cut or mature forest (Table 8). Diurnal species predominate in both sites with herbaceous canopy, but nocturnal species predominate in mature forest (Table 8). Forty-six species of beetles were collected more than 10 times; 37 less frequently (N = 12 traps/community - Table 9). Seventy-eight percent were collected in clear-cut and/or GTR, 33% of these were found in mature forest as well. Twenty-four percent of the common species were restricted to a single community type (clear-cut = 1; GTR = 6; mature forest = 4). Eighty-four percent of the rarer taxa were found either in GTR or mature forest. All of the commonest taxa are either widely distributed throughout all three community types or are restricted to the clear-cut and GTR (Table S5).

Soils

The soil faunas were of three types: (a) clearcut$_2$ and both GTR sites dominated by endeostigmatid mites; (b) clearcut$_2$ dominated by springtails (only one species) and endeostigmatid

mites; and (c) both forested sites dominated by oribatid and predaceous mites. Mesoarthropods of all feeding types dominated in mature forest. Total census count: severely-burned clear-cut > mature forest > GTR > weakly-burned clearcut (Table 10).

Total soil fauna biomass is 5-16 fold greater in mature forest than in any open community (Table 11). Even subtracting the infrequent mesoarthropods, mature forest is 2-6 fold greater in soil fauna biomass. Even though oribatid mites are relatively infrequent out of the mature forest, they comprise 10-33% of the community biomass; though far more abundant in the forest, the presence of more mesoarthropods reduced their biomass share to 7-9%.

All non-rare soil fauna are widespread throughout all six sites, though relative abundances vary greatly: springtails - *Tetracanthella*; oribatids - *Carabodes*, *Caenobelba*, *Ceratozetes*, *Hermaniella*, *Oribatula*, *Euphthiracarus*, *Oribotritia*, *Maerkelotritia*, *Ceratoppia*, *Platynothrus*, *Liacarus*, *Xenillus*, *Galumna*; predaceous mites - *Zercon*, polyaspidids; pseudoscorpion - *Apochthonius*; protura; flies - Tipulidae, Sciaridae; beetles - Elateridae heavily prefer mature forest; oribatids - *Propelops*; endeostigmatids - *Nanorchestes* 2 spp prefer either clear-cut and GTR.

DISCUSSION

Two major observations are that:

a) different types of traps sample very distinct community segments (analogous to different hunting strategies of bird species); and

b) data from a single trap type reveals that the majority of non-rare species are shared between more than one community type.

Soils

Soil samples estimate the absolute density of arthropods within a microsite that could be harvested by a predator. Since most of these organisms are probably smaller than the threshold allowing exploitation by vertebrates, this fauna can be viewed as either an indirect determinant of epigeic macroarthropod biomass or in the more theoretical context of how much energy is being actively cycled through these food web components in these differing community types. Data presented above imply that the severity of burning has a greater impact on abundance than retention of green trees, because there is greater disparity within the replicates of the same community type than between clear-cut and GTR.

Burning subsequently impacts the soil fauna in two principal ways: (a) removal of habitat (physical elimination of litter); and (b) alteration of resource base (fungal-dominated ecosystem food web in unaltered litter changes to bacterial-dominated food web in dense annual grasses and forbs - Ingham and Thies 1995). Clear-cutting (with or without occasional GTR) reduces soil fauna, both microarthropods and mesoarthropods, to levels far

below those characteristic of mature forest, and facilitates a major shift away from fungivorous oribatid mites and predaceous gamasid mites towards endeostigmatid mites (diverse poorly known feeding habits). The enormous abundance of *Onychiurus* in clearcut$_2$ was unexpected. In many years of sampling soil fauna from clearcuts (Moldenke 1996a, 1996b, & unpublished data), we have never seen a similar population explosion of springtails. However, we have never sampled a clearcut with: (a) such luxurious weedy herbaceous annual regrowth following such a (b) severe broadcast burn. Such clearcuts are common in practice. The *Onychiurus* response is equally pronounced in 5 of the 6 subsites sampled and is presumably generally characteristic of that site. This enormous abundance occurs throughout a region devoid of any visible litter layer, leading us to question what the resource base is. The only likely possibility is the root hairs of grasses and forbs; though normally considered hyphal feeders, frequently grazing on mycorrhizae, springtails have been recorded to feed on roots themselves.

The twelve individual replicates from the second GTR site show considerably more point to point variability than the first site. The majority of the first site was not burned during harvest; the second site was both pile burned and sections broadcast burned. We expect the microarthropod variability reflects altered levels of residue litter and CWD.

The sample sizes, though sufficient to yield robust estimates for microfauna, were inappropriate for mesofauna. Soil

mesofauna would be more appropriately measured with 25 x 25 cm Berlese samples.

Pitfalls: the ground feeder resource

The macroarthropod epigeic fauna is much greater in clear-cut than GTR than mature forest, whether analyzed compositely or separately into both diurnal and nocturnal components; this pattern is true for individual census count, biomass and species richness. The great majority of the biomass in either closed-canopy or open-canopy communities is comprised of only a few widespread species. These species are present nearly all year long and may represent sufficiently predictable resources to allow facultative specialization by predators. Individual taxa will predictably cycle in size-class availability/abundance differentially throughout the year (e.g., grasshoppers - extremely abundant but small in spring, decreasing in abundance but increasing in size and mobility until the mid-dry season; wolf spiders with adults peaking in spring, followed by a period of minute spiderlings, building in size until the fall frosts - McIver et al, 1992). Diurnal birds, lizards (*Sceloporus*, *Gerrhonotus*) and snakes and some of the predaceous prey base itself will compete for this resource.

The prevalence of diurnally-active arthropods in open-canopy but of nocturnally-active taxa in the mature forest should fundamentally permit bird predation in clearcuts (and forest canopies) and mammal insectivory in forests, largely exclusive of one-another. However, total arthropod biomass is not directly

equivalent to food availability. *Harpaphe* is not the only species with predator-avoidance attributes. Most of the larger arthropods (e.g., stinky ground-beetles, spider venom, regurgitating Orthoptera) are to some extent differentially repulsive to the spectrum of vertebrate predators. To estimate prey preference distinctions, sample vertebrate guts need to be examined seasonally, while *simultaneously* sampling total prey abundance. Only in this comparative fashion can prey availability be translated into food availability.

Sticky traps: the flycather resource

Flying flotsam availability is significantly higher in open canopy situations than in closed forest sites, with GTR exceeding clear-cut. The most abundant taxa collected were sciarid gnats, chironomid midges, ceratopogonid flies and click beetles -- all of which are most likely dependent upon an undisturbed litter layer. Both the clear-cut and the GTR site with the more severe burning showed far lower populations of flying insects than their counterpart.

Though the size classes decrease logarithmically in abundance, even the smallest midges seem to be highly visible to flycatching birds and bats. Flight periods for most of the smaller dipterans are not well understood, but enough information is available to provisionally assign general flight periods for most of the beetle species. Diurnal fliers are far more abundant in open-canopy situations, nocturnal species in mature forest; this trend parallels that of epigeic pitfall results.

Unlike the pitfall results where clear-cut > GTR in most analyses, GTR > clear-cut in sticky trap results. Though only 33% of the species are shared between GTR and mature forest, the most abundant species are all shared. The more limited mobility (walking) of the epigeic macroarthropods yields results probably not too different from expectations within an extremely large clearcut, however, the high vagility (e.g., flying) of sticky trap insects combined with the small area (ca. 40 acres) of the clearcuts produces an amalgamation of both open canopy and closed canopy residents. Our sample points were at the center of the clearcut; it would be intriguing to know the distribution of "flycatcher resource" as one crosses the boundary ecotone, since it is along this boundary that the maximum number of perching sites are located for flycatching birds.

Beating/Sweeping; the foliage gleaner resource

In one perspective, the beating samples were not successful in that they were not extensive enough to produce clear-cut differences; within sample variability was large. Though we in this sense "failed to show differences" between the community types, which presumably do exist at some level, we did show that there were large resources in all three areas. Unlike pitfall and sticky traps which accumulate individuals over three-week periods and do not attempt to estimate instantaneous availability (undoubtedly highly weather dependent), beating/sweeping estimates resident densities.

A big question in our minds, is what of these resources are actually available to potential vertebrate predators. It seems unlikely that vertebrates could efficiently exploit the smallest size category. This is due to both (a) crypsis and (b) harvest difficulties. Though we expect that most birds, mammals and reptiles would prey on these organisms in laboratory feeding trials, in Nature on disruptive backgrounds their visibility decreases and many inhabit microhabitats (leaf extremities, flowers) that so deform under the weight of vertebrates that frequent capture is precluded. What are the variables which determine which microhabitats effectively preclude vertebrate predation?

Size-class distribution of prey items is critical at all times, but especially so during the breeding season. Annual grasses and forbs often support a higher ratio of herbivores : gross primary productivity than other plants, since as a general rule they are less protected by secondary chemicals. The seasonality of the growth cycle limits most of the herbivores to fall reproduction, hence in the spring bird nesting season most species are small immatures, more likely to escape detection by foraging adult birds. On the other hand, herbivores utilizing sclerophyllous shrubs and evergreen conifers are frequently restricted to early spring for the completion of larval development, before the perennial leafs start to produce secondary chemicals. Hence, during the nesting season the larger size classes of prey are usually well-represented in forest canopies and understories. Our samples were taken after fledging

and missed the peak of caterpillar production. Forest $sample_1$ is likely to be more depauperate than $sample_2$, because the vegetation was nearly exclusively a single canopy of monoculture *Gaultheria*; $site_2$ was characterized by a multi-layered diverse shrub and herb layer.

Based on years of anecdotal field observation, we postulate that the availability of large-sized arthropods decreases drastically in the forest understory as the growing season progresses, yet increases in clearcuts. We, therefore, expect that mobile bird gleaners should shift the majority of their feeding to clearcuts in the summer after fledging occurs.

CONCLUSIONS

We conclude that it is possible to attain first order estimates of food availability for vertebrate insectivores by the use of several types of low-input low-cost trapping devices. We caution, however, not to extend the numerical results obtained in this study to other seasons of the year. Vertebrate ecologists are often unfortunately remarkably ignorant of insect biology. The great majority of our resident forest birds derive a significant portion (10%? to 90%?, what is it?) of their *nourishment* from insects as immatures, but to hang an "insectivore" label on them in a comparative table, conveys little information more than that they do indeed feed (which we had presumed all along to be the case). Certainly, there are lots of kinds of insects in the environment of a bird species, but

only a very few make a significant contribution to a species' diet during any period. During those periods when $insect_A$ is abundant, we should expect a vertebrate to alter its foraging behavior to facultatively specialize on $insect_A$, etc. Even flycatchers, which theoretically should be the most species-blind predators, should alter height locations, ecotone positions and times of activity as the flight seasons of major insect biomass contributants sequentially succeed one another.

Differential insect abundance and species richness is greatest comparing closed- and open-canopy conditions. This is hardly surprising since one is comparing fundamental "apples and oranges". The notable increase in insect abundance and diversity in clearcuts over forests is an artifact in our study of comparing an entire community (clear-cut) with only a single stratum (ground level to 2m in mature forest). However, clearcuts are far from the "species wastelands" they are represented to be by certain politically active groups. Though no directly relevant data exist to compare the full ecosystem species richness between clearcuts and forested conditions, we expect that the early stages of forest succession are more species-rich than some closed-canopy stages. We know that for the epigeic and subsoil components, species richness falls during the middle stages of forest regeneration; rising again during later stages when CWD is again being added to the litter and gaps are imposing spatial heterogeneity on the landscape (Moldenke & Fichter 1988, McIver et al 1992).

The results presented in this paper highlight the importance of other variables in determining insect abundance and diversity. Different forest types develop with different trajectories of habitat heterogeneity. There is far less foliage-gleaner resource available in normal forest types with uniform or no understory layers. Habitat resource is also crucial in clearcuts. Vertebrates cannot forage without prey; prey is dependent upon food resources, a medium in which to live, and microsites to avoid desiccation. Severe broadcast burning removes these necessities for most species, yet indirectly it creates its own resources (annual plant forage). It is necessary to further quantify the effects of habitat structure in a careful factorial experimental design before pronouncing judgement of the relative merits of a management practice such as "GTR".

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census count				biomass		
CC	GTR	MF		CC	GTR	MF
30a	142b	67a	millipedes	11769	100561	39434
351c	109b	65a	beetles	103626c	24719b	7283a
56	43	63	Orthoptera	20886	21376	14110
172b	203b	77a	spiders	10078b	10952b	3514a
37	7	20	chilopods	4640	2647	6255
172	203	77	spiders	10078	10952	3514
26	4	5	caterpillars	8545a	1900b	903b
107b	20a	11a	skunk-spiders	7595b	282a	232a
34	20	24	wasps	3179b	428a	240a
4	14	21	Thysanura	64	224	336
0	5	6	Isopoda	0	85	102
494b	200b	0a	ants	4449c	1965b	0a
135b	68b	1a	Hemiptera	658b	371b	9a
1450b	836a	360a	SUM	175693b	165570b	72418a
			sum - millip	165493b	88220ab	48618a

Table 1. Epigeic macroarthropods collected in pitfall traps. Numbers on the left represent sums of 6 census counts; numbers on the right represent the sum of six replicate traps in biomass (ug). The major taxa of epigeic arthropods are listed separately, as well as the total of all taxa, and the biomass total minus the contribution of *Harpaphe*. ($p < 0.01$)

census				count		
				biomass		
CC	GTR	MF		CC	GTR	MF
494b	200b	0a	ants	4449b	1965b	0a
117b	2a	0a	beetles	1313b	14a	0a
135b	163b	51a	Hemiptera	768b	318b	9a
26	4	5	caterpillars	8545b	601a	903a
12a	123b	33a	millipedes	9000	81050	23000
48b	29b	0a	Orthoptera	13018b	18281b	0a
158b	173b	68a	spiders	17074b	14187b	4130a
4	14	21	Thysanura	64	224	336
34	20	24	wasps	8210b	4190b	240a
998b	628b	152a	SUM	54167	116411	28042
			sum - milli	45167b	35361b	5042a

Table 2. Pitfall data reporting only diurnal species. Format as in Table 1. ($p < 0.01$).

PITFALL TRAP DATA

CC	GTR	MF	common species	rare species
+	-	-	4	51
-	+	-	0	27
-	-	+	4	16
+	+	-	19	12
-	+	+	4	5
+	-	+	0	0
+	+	+	16	0
			47	111

39	39	24	common species
63	44	21	rare species
102	83	45	TOTAL species

Table 3. Species richness represented in pitfall traps with indication of stand type distribution. + indicates species is present; - indicates absence.

BEATING / SWEEPING DATA

CC_1	CC_2	GTR_1	GTR_2	MF_1	MF_2	
153a	136a	149a	127a	72a	348b	0.0-2.5mm
67	222	118	97	69	161	2.5-5.0mm
36a	82a	151b	58a	31a	52a	5.0-7.5mm
52	86	52	29	12	49	7.5-10.0mm
10	30	17	15	2	1	10.0-12.5mm
10	12	16	5	3	3	12.5-15.0mm
5	3	13	4	2	6	15.0-17.5mm
0	0	0	0	0	0	17.5-20.0mm
0	0	0	0	0	2	20.0-22.5mm
0	0	0	0	0	3	22.5-25.0mm
1	0	0	0	0	1	25.0-27.5mm
1	0	0	0	0	2	27.5-30.0mm
25	64	47	72	30	52	beetles
34b	450c	79b	128c	9a	42b	Hemiptera
47a	30a	139b	59a	77a	214b	spiders
335a	571b	516b	335a	191a	628b	SUM all taxa

Table 4. Size class distribution of potential prey items collected by beating and sweeping. Census totals for the three most important taxa cited. All numbers represent total specimens collected in six replicate samples. ($p < 0.01$)

SPECIES RICHNESS IN BEATING/SWEEPING SAMPLES

sums of species in each of 6 reps							u species richness per comm type		
CC_1	CC_2	GTR_1	GTR_2	MF_1	MF_2		CC	GTR	MF
19	16	18	25	18	27	beetles	2.9	3.6	3.8
11	59	24	35	8	8	Hemiptera	5.9	4.9	1.3
34	18	35	36	47	57	spiders	4.3	5.9	8.7
64	93	76	95	73	92	all taxa	13.1	14.3	13.8

Table 5. Species richness represented in beating/sweeping samples. Left-hand numbers represent the sum of the total species in each of six replicates (therefore the same individual species can be scored in different samples). The right-hand numbers represent the total different species in each of the two stands per community type divided by two.

BEATING/SWEEPING RESULTS

CC	GTR	MF	common species	rare species
+	-	-	8	19
-	+	-	5	18
-	-	+	7	20
+	+	-	15	8
-	+	+	10	2
+	-	+	0	0
+	+	+	8	0
			53	67
31	38	25	common species	
27	28	22	rare species	
58	66	47	TOTAL species	

Table 6. Species richness represented by beating/sweeping captures with indication of stand type distribution. + indicates species is present; - indicates absence.

STICKY TRAP CAPTURES
size classes

CC_1	CC_2	GTR_1	GTR_2	MF_1	MF_2	
2355	2560	8710	4611	482	1098	0-5mm
433	965	970	578	665	424	5-10mm
85	121	128	70	253	113	10-15mm
26	9	9	6	20	19	15-20mm
6	0	0	1	0	51	20-25mm
0	0	3	0	0	0	25-30mm
235	353	1294	313	411	118	beetles only
2905	3655	9820	5266	1420	1705	SUM
6560		15086		3125		

Table 7A. Size-class distribution of sticky trap captures. Numbers represent the sums of six replicate samples.

CC_1	CC_2	GTR_1	GTR_2	MF_1	MF_2	
176c	263d	324d	88bc	38ab	18a	diurnal beetles
430b		412b		56a		
68a	90a	970c	225ab	373b	100a	nocturnal beetles
158a		1195c		473b		

Table 7B. Diurnal and nocturnal beetle component in sticky trap results. Numbers represent the sums of six replicate samples. ($p < 0.05$)

STICKY TRAP RESULTS

CC_1	CC_2	GTR_1	GTR_2	MF_1	MF_2	
19	19	24	23	7	8	diurnal
10	15	21	14	17	16	nocturnal
29	34	45	37	24	24	SUM
22		32		12		diurnal
17		25		27		nocturnal
39		57		39		SUMS

Table 8. Species richness of beetles in sticky trap results. Topmost series of numbers represent the sum of the total species in each of six replicates (therefore the same individual species can be scored in different samples). Bottom numbers represent the total number of different species collected within a community type (N = 12 samples).

STICKY TRAP CAPTURES

CC	GTR	MF	common species	rare species
+	-	-	1	5
-	+	-	6	15
-	-	+	4	16
+	+	-	17	1
-	+	+	6	0
+	-	+	0	0
+	+	+	12	0
			46	37
30	41	22	common species	
6	16	16	rare species	
36	57	38	TOTAL species	

Table 9. Species richness represented by sticky-trap captures with indication of stand type distribution. + indicates species is present; - indicates absence.

SOIL CORE SAMPLES

CC_1	CC_2	GTR_1	GTR_2	MF_1	MF_2	
57a	1901b	94a	173a	166a	229a	springtails
176a	195a	380a	151a	1156b	1023b	oribatid mites
14a	11a	15a	3a	53b	78b	predaceous mites
378ab	772b	460ab	56ab	104ab	1a	endeostigmatids
8bc	0a	3ab	3ab	8bc	14a	herbivorous ins
8ab	0a	4ab	1ab	18b	46c	predaceous ins
13a	7a	9a	4a	59b	52b	fungivorous ins
654	2886	965	903	1564	1443	SUMS
3540		1868		3007		

Table 10. Fauna of soil samples (per $25cm^2$). Numbers represent the totals collected in a total of twelve replicates. ($p < 0.0005$). (CC_2 = severely burned)

SOIL CORE SAMPLES

CC_1	CC_2	GTR_1	GTR_2	MF_1	MF_2	
612a	22802b	1205a	2247a	3136a	6804a	springtails
10363ab	3678a	7474ab	1612a	16511bc	24747c	oribatid mites
2740a	1220a	1547a	215a	14337b	18446b	predaceous mites
378	772	464	568	112	1	endeostigmatids
14093b	28472b	10690b	4642a	34096c	49998c	SUM allmicrotaxa
x=21282		x=7666		x=42047		
5430abc	0a	1860ab	1710ab	5860bc	8880c	herbivorous ins
53900a	0a	1270a	500a	81725a	246220b	predaceous ins
4190a	2875a	7715a	3300a	35565b	42185b	fungivorous ins
77613a	31347a	21535a	10152a	157246b	347283b	SUM all taxa
x=54480		x=15843		x=252264		

Table 11. Biomass (ug/25 cm^2) of soil fauna. Numbers represent the totals collected in twelve replicates. ($p < 0.01$)

APPENDIX 1. Stand type preferences of key taxa
1=pitfall; 2=beating; 3=sticky trap

clear-cut CLEARCUT DOMINANTS ONLY
BEETLES
Amara spp1
Calosoma tepidum1
Necrophilus hydrophiloides1
HEMIPTERA
Orius tristicolor2
Stenodema vicina2
Megalonotus sabulicola2
Malezonotus sodalicus2, obrieni2
Anthocoris sp2
GRASSHOPPER
Melanoplus lepidus2
CATERPILLAR
Pyrrharctia isabella1
SPIDERS
Phidippus johnsoni1
Sassacus pappenhoei2

DOMINANTS IN GTR GREEN RETENTION SITES ONLY
BEETLES
Lepturopsis dolorosa3
Silis spp2
SPIDER
Oxyopes scalaris2

DOMINANTS IN mature forest FORESTED PLOTS ONLY
BEETLES
Podabrus sp2
Leptura obliterata3
Ampedus nigrinus3
SPIDERS
Antrodiaetus pacificus1
Cybaeus spp1
Metellina mimetoides2
Nuctenea patagiata2
Neriene digna2
Prolinyphia sierrensis2
Theridion 3 spp.2

DOMINANTS IN clear-cut + GREEN TREE RETENTION
BEETLES
Harpalus cautus1
Nicrophorus defodiens1
Pterostichus amethystinus1
Coccinella trifasciata2
Rhynchites bicolor2
lathridiid2
Neomysia subvittata3
Buprestis aurulenta3
Cycloneda polita3

Dermestes talpinus3
Diabrotica 20-maculata3
Bromius obscurus3
Hippodamia convergens3
Mordella atrata3
Trichodes ornatus3
ANTS
Camponotus modoc, noveboracensis1
Formica pacifica, subnuda1
HEMIPTERA
Geocoris pallens2
Lygus spp.2
Nabis alternatus2
Nysius niger2
Psallus sp2
Lopus discolor2
Euschistus conspresus2
Malezonotus grossus1
Eremocoris dimidiatus1
Scolopostethus pacificus1
Neides muticus2
SPIDERS
Araneus diadematus2
Dictyna peragrata2
Xysticus gosiutus2
Lycosa sp1
Pardosa mackenziana1
blkgnaf1
WASPS
Pompilidae 8 spp.1

DOMINANT IN GREEN TREE RETENTION + mature forest
BEETLES
Anaspis rufa2,3
Malthodes spp2
Hylis terminalis3
Troglomethes oreganus2
Thanasimus undulatus3
Ctenicera comes3
Xestoleptura crassipes3
Evodinus monticola3
TERMITE
Zootermopsis angusticollis3
MILLIPEDE
Tylobolus deces1
ISOPODA
Ligidium gracile1
OPILIONID
Dendrolasma mirabile1
HEMIPTERA
Kleidocerys 2spp2
Banasa sordida2
SPIDERS
Theridion lawrencei2

Antrodiaetus occultus1
Misumenops celer2
Cyclosa conica2
Pityohyphantes rubrofasciata2
Philodromus rufus, spectabilis2

DOMINANT SPECIES IN ALL 3 COMMUNITY TYPES
BEETLES
Pterostichus herculeanus, lama1
Steremnius carinatus1
Psyllobora 2spp2,3
Megapenthes caprella2,3
Aphodius opacus3
Ctenicera 2 spp3
Mycetochara procera3
Xestobium affine3
Cephaloon tenuicornis3
SPIDERS
Araniella displicata2
Clubiona canadensis2
Metaphidippus aeneolus2
Misumena vatia2
Araneus gemmoides2
Cybaeus reticulatus1
HEMIPTERA
Jalysus wickhami2
CENTIPEDE
Scolopocryptops sp1
MILLIPEDE
Harpaphe haydeniana1
Nearctodesmus sp1
ORTHOPTERA
Pristoceuthophilus cercalis1
BRISTLETAIL
Machilid1
OPILIONID
Leuronychus parvulus1
SNAIL
2spp1

SUMMARY

Retrospective Study

The results of the retrospective study suggest what some of the longer-term implications of green tree retention may be. With respect to the tree layer, the presence of residual trees at basal areas roughly comparable to amounts currently prescribed for Federal forests in western Oregon and Washington was associated with significant decreases in basal area, volume, current volume growth rate, and mean annual increment of the younger cohort. This level of residual basal area was also associated with a significant decrease of the combined basal area growth of the younger cohort and residual trees. We did not find significant relationships between residual trees and height or density of the younger cohort, an index of younger cohort tree mortality, or total live standing volume (younger cohort plus residuals).

Relationships between residual trees and the components of biodiversity we examined were both indirect and direct. For understory herbs and shrubs, responses were mediated through effects of residual trees on the younger cohort of trees. Herb and shrub cover and species richness tended to increase with increasing Douglas-fir in the younger cohort, which was associated with fewer residual trees, drier sites, and lower density of the young cohort. Biomass of cyanolichens increased with increasing numbers of residuals and also with an increasing proportion of western hemlock in the younger cohort. Biomass of forage and green-algal foliose lichens decreased with increasing density of the younger cohort. Total basal area of residuals was positively associated with biomass of green-algal foliose lichens; the proportion of surrounding area comprised of older forest was positively associated with biomass of forage lichens. Based on these results we expect green tree retention to have positive effects on forage lichens and

nitrogen-fixing cyanolichens.

Results from the retrospective study should be interpreted in light of several strengths and limitations. Strengths of the retrospective study include the pairing of plots with and without residual trees, the broad geographic spread of plots, and the narrow range of plant association types represented. The inclusion of 14 matched pairs of plots within the western hemlock zone minimized confounding sources of variability between plots and accentuated differences correlated with residual trees. The 14 pairs of plots were well-distributed across the Willamette National Forest, with five of the seven Districts represented. Despite the geographic spread of the pairs in the western hemlock zone, all occupied one of three closely related plant association types (presumably representing a narrow range of environments), again minimizing extraneous sources of variation.

Limitations of the retrospective study include both problems common to all retrospective studies and concerns specific to this study. As in all retrospective studies, there was no control over the disturbances that initiated the stands or detailed information on the nature of those disturbances. Similarly, the spatial distribution of residual trees, an important feature of green tree retention harvest systems, could not be controlled. A specific problem of this study was the relatively small sample size. The regeneration cohort had relatively high stocking compared with that found in most managed stands. Finally, since few of the plots with residual trees contained very low numbers of residual trees, little can be said based on this study concerning likely effects of low levels of green tree retention.

Studies in Recent Green Tree Retention Units

The frequency of mycorrhizal mats was greater near living host trees in control stands, with evidence from green tree retention cuts that mats may persist for at least 2 years after their host trees have been cut. Ectomycorrhizal diversity on Douglas-fir seedlings planted near or far from green trees, however, showed no clear patterns of influence by the retained tree. This was likely due to the high fungus inoculum potential of the recently cut sites. Different functional groups of arthropods had different patterns of abundance across a range of stand structures, including recent green tree retention cuts, clear cuts, and mature forests. Biomass of flying arthropods was greater in green tree retention cuts than in the other two stand types (favoring avian predators). In contrast, biomass of ground-dwelling macroarthropods was highest in clearcuts; biomass of soil microarthropods peaked in mature forests. Again, effects of residual trees on biodiversity differed for different functional groups of species.